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Anti-predator behaviour of cape fur seals *Arctocephalus pusillus pusillus* in relation to predation by white sharks *Carcharodon carcharias* around Seal Island, False Bay, South Africa

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Alta De Vos

Illustration: SZABOLCS KÓKAY

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Opgedra aan my ouers en ter herinnering aan Magriet

Abstract

How predators affect the behaviour of their prey is one of the most studied subjects in behavioural ecology, with many hypothesis and models explaining how animals should behave and even more descriptive studies detailing how they do. The unification of the empirical with the theoretical, however, remains limited. The overall aim of my thesis was to address this paucity at Seal Island, South Africa, where recently quantified patterns of predation pressure by white sharks *Carcharodon carcharias* on Cape fur seals *Arctocephalus pusillus pusillus* suggested a landscape of fear particularly apposite to this. I started this study by describing spatiotemporal seal behaviour in relation to these predation events, which revealed two patterns suitable to theoretical investigation. First, leaving groups avoided the elevated pulse of risk immediately following sunrise. In keeping with the risk allocation hypothesis, which predicts how animals should behave when predation risk vary temporally, I subsequently found evidence that both adults and initially naive juveniles (these seals accounted for nearly all attacks observed after sunrise) adjusted their behaviour in relation to predation risk: adults from winter (high risk) to summer (low risk) and juveniles from early winter (naive) to late winter (more experienced). Second, initial patters of grouping at the island revealed that single seals were at higher risk than individuals in groups, and that individuals were loosely aggregated in summer, but “jostled” in compact herds in winter. This invoked the selfish herd hypothesis, an often-cited, but virtually untested hypothesis. It predicts that groups form when animals move towards nearest neighbours to decrease their domain of danger, an area around them within which they are at risk to a randomly appearing predator. In an experimental test of the hypothesis, using seal decoys, I show support for the prediction that an individual’s domain of danger is proportional to its relative predation risk, and a in a subsequent analysis of seal herd movement trough the danger zone, I show that seals follow simple selfish herd rules, that this leads to reduced individual domains of danger and more compact groups within the danger zone. My study demonstrate the value of using novel systems as fresh approaches to long-standing problems, and integrating the theoretical and the empirical to concomitantly improve case-study understanding of ecosystems and the theoretical frameworks within which we seek to understand them.

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Declaration

I, Alta De Vos, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Alta De Vos

University of Cape Town

Acknowledgments

All successes, be they winning Olympic gold medals or somewhat smaller achievements like finishing a PhD write-up, are similar in some ways: they require hard work, some ability on the part of the executor, the right opportunities and the right people in support. Some people, being fiercely capable and tenacious, struggle against difficult odds to achieve their successes. Others, being of average capabilities, just know the right people.

I'm definitely one of the latter.

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and for providing me with more opportunities than I have the time to take advantage of.

My parents, Dirk & Lynn De Vos, deserve a special thank you: Dankie dat julle alles in julle vermoë gedoen het om my te help om my eie pad te volg, al moes julle in die proses baie harkoppigheid verdra. Ek het nooit vir een oomblik getwyfel aan julle ondersteuning en liefde nie, of dat julle net die beste vir my wou hê nie. Dankie aan al die ander De Vosse & Gerbers (en ekstensies) wat my aangemoedig het langs die pad (partykeer met ‘n preek of twee!). ‘n Groot dankie veral aan Cora-Marie De Vos, wat die beste kleinsus is wat enige iemand voor kan vra.

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Esme Beamish also deserves a special mention. Thank you for providing me with a roof over my head, one (two! If you count Churchaven) of the most beautiful write-up spots on record, many late-night chats over coffee, and some of the most fantastic dinners. Can not wait to show you Angola next year!

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Lastly, but not least: thanking God seems something that sportsmen do after He “helped their side win”. I do not believe that I’ve been “made to win””, but it is

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comforting and liberating to have a foundation from which one can question everything else. Contrary to popular perception, it is a very useful condition within which to train as a scientist, and a most solid position train for life. Not acknowledging this would certainly be dishonest.

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Chapter 1

Introduction

How can seals-shark interactions
inform predator-prey theory?

1.1. Predator-prey theory

Predators can shape the ecosystems in which they live by reducing prey densities, which in turn affect populations at lower trophic levels (Abrahams 1995, Mann and Watson-Capps 2005, Luttbeg and Kerbey 2005). Alternatively, but not mutually-exclusively, predators can affect prey populations in a non-consumptive manner, as anti-predator defences may manifest as changes in prey resource use, ultimately shaping community composition and dynamics (Lima 1998, Brown *et al.* 2001, Peacor and Werner 2001, Heithaus and Dill 2002, Khan and Ghaleb 2003, Werner and Peacor 2003, Schmitz *et al.* 2004, Preisser *et al.* 2005, Owen-Smith and Mills 2006, Verdolin 2006, Cresswell 2008). Understanding anti-predator defences thus represents an important step in understanding and contextualising ecosystems. At the same time, thorough ecosystem understanding is important in the general understanding of predator-prey theory.

Animals may show a great variety of behaviours when threatened by predators. These include using refuges (Sih *et al.* 1998, Hochman and Kotler 2007), releasing chemicals (Monclus *et al.* 2005), alerting con-specifics with alarm calls (Hollen and Manser 2006), increasing individual vigilance (Clutton-Brock *et al.* 1999; Uetz *et al.* 2002, Cresswell *et al.* 2003, Jackson and Ruxton 2006), grouping (Turchin 1997, Hass and Valenzuela 2002, Hebblewhite and Pletcher 2002, Viscido and Whetley 2002, Lett *et al.* 2004, Losos *et al.* 2004) and mobbing (Altmann 1956, Owings and Coss 1977, Stewardson and Brett 2000, Clark 2005). In addition, animals may adjust their foraging behaviour (Trouilloud *et al.* 2004), spatial, (Creel and Winnie 2005), temporal, (Lima and Bednekoff 1999) and social activities (Barta *et al.* 2004, Cameron and du Toit 2005) to offset predation. Comprehensive reviews on anti-predator defences have been completed for birds and mammals (Caro 2005), fish (Magurran and Pitcher 1987, Pitcher and Parrish 1993) birds (Cresswell 2008) and insects (Ruxton *et al.* 2004).

Attempts to understand the evolution and proximate role of defensive traits have typically viewed them in isolation of other potential causative factors for single response variables (Belovsky *et al.* 2004). However, in reality, defensive traits all interact within a landscape of fear (Thompson *et al.* 2006, Liley and Creel 2007, Wirsing *et al.* 2008) and it is thus necessary to investigate traits in the context of

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other ecological components (e.g. life history, foraging) before one obtains an improved biological understanding of any given trait. However, current ecological theory, to a large extent, is organised along the former approach and if we wish to contribute to it, disentanglement is required.

Ordering interactive "defence traits"

One way of conceptualising and artificially disentangling predator-prey interactions is by ordering encounters "chronologically" and listing defences in response to each phase of such an attack (Pitcher and Parrish 1993, Hileman and Brodie 1994). These "responses" mix evolutionary, ontogenetic and proximate timescales, with some defences operating at more than one stage of predation. The advantage this approach has over schematic approaches (e.g. Lima and Dill 1990, Martin *et al.* 2005) is that it considers anti-predator defences as alternatives to each other, which is less artificial than presenting prey with a sequence of possibilities to explore on a linear scale (Caro 2005).

There are a broad spectrum of approaches that could be employed to determine the number and emphasis of predatory attack phases and the defences they might incite (e.g. Edmunds 1974, Vermeij 1982, Endler 1991, see Caro 2005 for a review). I largely follow Edmunds (1974) simple splitting of defences into primary (indirect) and secondary (direct) categories. The distinction is that primary defences operate regardless of whether or not a predator is in the vicinity, while secondary defences operate during an encounter with a predator. Another popular framework for anti-predator defences is that of Endler (1991), where defences are listed as responses to six "phases of predation", namely: prey encounter (i.e. predators are sufficiently close to makeprey detection possible), prey detection, identification of prey targets, approach (attack), subjugation (preventing escape) and consumption. Primary defences reduce encounter, detection, identification and approach phases. Secondary defences overcome subjugation and consumption.

The importance of a theoretical framework

One of the requirements for a discipline to qualify as a science (Moore 1993, Mayr 1999) is that it is characterised by the steady improvement of theories, where theories are defined as a framework or system of concepts and propositions that

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provides causal explanations of phenomena within a particular domain (Scheiner and Willig 2008). Improvements come about through the replacement of faulty or incomplete theories and through the solving of previously puzzling problems. Problems should be solved and theories judged by means of repeated hypothesis testing of predictions made by such theories, and generalisations should be universally valid across the domain of a certain discipline (Moore 1993, Mayr 1999).

Theories are essential to the scientific integrity of ecology (Weiner 1995, Cooke 2005), but the application of theory within this discipline is difficult (Kareiva *et al.* 1989), largely on account of the autonomous scientific nature of biology (Mayr 1996). In this sense I consider “theories” to include all models (not descriptive mathematical models, but general hypotheses with testable predictions – e.g. the ideal free dispersion hypothesis, kin selection) that make up the contingency theories (e.g. island biogeographical theory, metabolic theory, inclusive fitness theory) that form the foundation of general ecological theory (as argued by Scheiner and Willig 2008, e.g. evolution).

In the physical sciences one can make accurate predictions using pure mathematical reasoning from general basic laws, or infer precisely defined general laws from observations, but this is rarely possible in biological sciences (Mayr 2004, Talley *et al.* 2003). Indeed many physicalist principles are considered obsolete by advocates of the autonomous view of biology (e.g. Ayala 1968, Mayr 1996, 2000, 2004, Talley *et al.* 2003). This view rejects concepts such as essentialism, determinism and reductionism from the biological realm, and replaces them with an acceptance of the frequency of random events, historical narrative (dual ultimate or evolutionary and mechanistic or proximate causation, is another autonomous feature of biology – Mayr 1996, 2004), population thinking and the greater importance of concepts rather than of laws (but see Scheiner and Willig 2008) in theory formation (Mayr 1996, 2000). The extent to which general theories are possible in what seems to be a science of specific solutions (Talley *et al.* 2003), and what this implies to its character is a much debated issue (Peters 1991, Cooper 2004, Scheiner and Willig 2008).

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These fundamental "identity issues" in ecology may ultimately be responsible for the emergence of two extreme (and one intermediate) practices of investigating "the science for the struggle of existence" (Cooper 2004). On the one extreme, there is the "constipating accumulation of untested models" (Schoener 1972), based on simple, realistic mathematical assumptions (Kareiva *et al.* 1989, Baklavov *et al.* 2004, Cooper 2004). These models may be considered to have deductive validity because they provide insight and capture essential features of a system, but their predictions may not be falsifiable (Weiner 1995), and in many cases lack biological realism (Baklavov *et al.* 2004). Some advocates of naïve Popperian falsification (e.g. Peters 1991) believe that these models cannot be considered theory at all. At the other extreme, is the "case-study" approach to the discipline – where data is collected without any theoretical question in hand and placed into a causal narrative backed up by statistical analyses to produce an air of understanding (Kareiva *et al.* 1989, Weiner 1995, Cooper 2004). Somewhere between these two extremes is the use of descriptive mathematical models (Cooper 2004). These are often considered adequate by the weak test of retrofitting to past data (Weiner 1995). These mathematical models often commit classic Ptolemaic over-fitting, with too many system-specific models producing too few useful hypotheses and predictions (Baklavov *et al.* 2004).

The difficulty in unifying the empirical with the theoretical and the purely mathematical in order to be able to make more general, unifying theories (Macfadyen 1975) remains a major challenge to ecologists (Kareiva *et al.* 1989, Baklavov *et al.* 2004, Cooper 2004). The need for parsimonious general explanations is increasingly urgent in a fast-changing environment where many problems may not allow a "case-by-case" approach. In the words of Baklovov *et al.* (2004) however, generality "cannot be declared – it has to be found" (Baklovov *et al.* 2004). This can only be done through the collection of data and the construction of deductive mathematical models to analyse patterns. Here the role of theory is to guide our thinking on how to ask questions, collect data and find patterns (Weiner 1995). Descriptive "case study" investigations and deductive mathematical models (especially as calculation tools – Weiner 1995) thus play as important a role in the theoretical scientific practice of ecology as theoretical ecology has to play in the understanding of individual and variable ecosystems. It is the integration of the

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theoretical with the empirical,, the relative contributions of these to each other and the correct levels of their relative application that remains the challenge (Kareiva *et al.* 1989, Belovsky *et al.* 2004).

Theoretical approach adopted in this thesis

I aim to combine the elements of ecological investigation, described above, to contribute to the understanding of the specific system under study as well as to hypotheses based on theory, by integrating descriptive pattern recognition, fitting data retrospectively to specific models, and testing hypothesis of long-standing theory. These hypotheses (or models - Scheiner and Willig 2008) make predictions that are considered to have general application in their specific domains. Through descriptive pattern recognition I aim to identify hypotheses that make predictions that are testable in the system under investigation. I further aim to improve these theoretical contributions by contextualising them within the ecology of the system under investigation.

Of particular significance is the fact that this system is a marine one, and marine ecology has been especially guilty of neglecting theory (Duarte 2007). The transfer of ecological theory across the land-ocean interface can be challenging because many underlying principles may be specific to terrestrial biomes (Churin *et al.* 2006). However, marine ecosystems may also offer novel opportunities to gain insight into difficult problems associated with ecological theory, traditionally applied to terrestrial systems (Steele 1991, Duarte 2007). In keeping with other studies that are recognising this potential (e.g. Duarte 2007, Laroche *et al.* 2008, Wirsing *et al.* 2008), this study represents an empirical attempt to breach this divide.

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In the remainder of this chapter I introduce the system under investigation, sketching the landscape of fear as defined from previous studies. I discuss the theory appropriate to the defined risk gradients (within the “disentangling” frameworks of Edgar (1974) and Endler (1991)), and outline the challenges posed by confounding variables in the ensuing data chapters.

1.2. The landscape of risk

White sharks (*Charcarodon carcharias*) are known to prey upon pinnipeds throughout their distributional range, a predator-prey relationship that probably dates back to when the ancestral *Enaliarctidae* re-entered the water *ca.* 20 million years ago (Maisey 1984, Wynen *et al.* 2001). The contemporary interactions of sharks and pinnipeds have been documented in many studies (e.g. Le Boeuf *et al.* 1982, Tricas and McCosker 1984, Ainsley *et al.* 1985, McCosker 1985, Klimley *et al.* 1992, 2001), but the conclusions drawn have been limited, predominantly because predation events can be difficult to observe (Ainsley *et al.* 1981, 1985, Tricas and McCosker 1984, Klimley *et al.* 1992, 1996). Seal Island, False Bay is quite different in this respect and Martin *et al.* (2005) reports a mean of 5.6 attacks per day) during the high predation season.

"The high predation season" equates to the austral winter, between the months of May and September – a time when white sharks aggregate around the breeding rookeries of the Cape fur seal (*Arctocephalus pusillus pusillus*) on the south coast of South Africa (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008). At Seal Island sharks leave the island in October, moving to the inshore region of the mainland, presumably to feed on fish (Kock and Johnson 2006). Shark activity around the island has only very recently been quantified (Kock 2002, Martin *et al.* 2005, Kock and Johnson 2006, Laroche *et al.* 2008), but basic predation patterns are now relatively well-established.

Sharks predominantly attack surface swimming seals from depth. Adult female seals typically feed far from the island, but being central place foragers, have to return to the rookery at regular intervals to feed their young of the year (David and Rand 1986). The young themselves venture out to sea at the start of the austral winter to supplement their milk-based diet (David and Rand 1986, Laroche *et al.* 2008). Shark attacks consist largely of surprise breaches on these juvenile seals when they are returning to the island, an attack which often results in sharks launching their entire bodies out of the water (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008).

The element of surprise appears to be important to the predation success of the sharks. Martin *et al.* (2005) found that more than 70% of attacks lasted less than

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one minute, and that first time breaches constituted 80% of all successful attacks (success rates vary between investigators – Martin *et al.* report 47.3%, Kock and Johnson (2006) report 51%). Prior to launching these attacks, sharks swim in the mid-water column (Laroche *et al.* 2008), concentrating their searching activity to the south and west of the rookery (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008). These sectors are also where most attacks are recorded (Kock 2002, Martin *et al.* 2005).

Attacks are not homogenous in time and space and not all seals are attacked equally. Most attacks happen in the first two hours after sunrise (Martin *et al.* 2005, Laroche *et al.* 2008) within 400m of the island (Kock 2002, Martin *et al.* 2005). Most victims are solitary, juvenile seals (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008). Spatially, sharks concentrate their attacks in the deep water around the south western side of the island (Martin *et al.* 2005, Laroche *et al.* 2008) and attacks are rare in the narrow skirt of shallow “safe zone” (Laroche *et al.* 2008) immediately adjacent to the island.

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Gradients of risk

Current predation patterns, in conjunction with bathymetry of the island and its relative position within False bay, equate to four categories of risk gradient which I will discuss in “chronological” sequence (*sensu* Edgar 1974, Elgar 1991):

(i) Spatial gradients of risk:

Seals are frequently attacked within 1.5km of the island, but only rarely beyond this (Kock 2002, Martin *et al.* 2005). There is also a safe zone immediately next to the island (without food resources, but potentially important for behavioural thermoregulation). Furthermore, attacks on seals are common on the south coast of South Africa, but very rarely observed at west coast colonies (Kock and Johnson 2006), resulting in a regional risk gradient (a third spatial gradient of risk).

(ii) A temporal gradient of risk:

Seals are mostly attacked within two hours of sunrise, with attack frequency decreasing as the morning progresses (Martin *et al.* 2005). Less than 13% of attacks occur after 10:30am and attacks may be completely absent at night (Martin *et al.* 2005).

Futhermore, marked seasonal variation in predation risk is apparent at south coast colonies with the austral winter being characterised by excepetionally high predation rates relative to summer months. The "spatial and temporal risk gradients", both at Seal Island on the south coast and relative to rookeries on the west coast provides an opportunity for predator-free "control" conditions with which to compare the behaviour and movement patterns of seals experiencing high predation risk.

(iii) A group-size dependent risk:

Not all seals are attacked equally. Single seals are attacked far more frequently than grouped seals (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008).

(iv) An age-class risk gradient:

Juveniles are attacked far more frequently than adults (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008).

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1.3. Defences geared at avoiding detection (*sensu* Endler 1991)

1.3.1. Spatial activity shifts (in relation to spatial gradients of risk)

Many empirical studies have shown that spatially localised predation risks can result in a shift of prey habitat use, even when this shift incurs an energetic cost or is associated with other constraints. For example, elk (*Cervus elaphus)* use wooded areas sparingly when wolves (C*anis lupus)* are present (Creel *et al.* 2007, 2008), kentish plovers (*Charadrius alexandrines)* select thermally-constraining nest-sites in the open where predators can be detected more easily (Losos *et al.* 2004), many herbivores avoid waterholes frequented by lions (*Panthera leo)* (Valeix *et al.* 2009), open-habitat hunting cheetah (*Acinonyx jubata)* restrict their movement to more bushy habitat with lower lion densities (Mills and Gorman 1997, Mills *et al.* 2004), and bluegill sunfish, *Lepomis macrochirus* undergo pronounced shifts in habitat use as they grow in response to changes in their vulnerability to predators (Mittelbach 1985).

Intuitively then, one might expect that prey would prefer to use safer habitats. This type of movement may, however, not be of much benefit to a prey individual when predator and prey species are both mobile, as benefits gained from "safe" habitat use are unlikely to be evolutionary stable (Sih 1984, 1998). The three-trophic-level ideal free dispersion model (Hughie and Dill 1994, Sih 1998), for example, predicts that prey should aggregate in patches with more resources, and predators should overmatch them there (Lima and Dill 1990, Hughie and Dill 1994, Sih 1998, Brown *et al.* 2001, Flaxmon *et al.* 2009). At Seal Island we investigate the spatial activity of seals in relation to higher frequency of attacks in certain areas around the island.

Refuges and safer habitats

Animals can restrict their activity to places of greater relative safety (usually refuges) in the presence of predators (Krivan 1998, Ylonen *et al.* 2003, Caro 2005). These may take the form of physical structures, such as trees (Cowlishaw 1997, Dill *et al.* 1997), bolt holes (Holmes 1984, Clutton-Brock *et al.* 1999, Sundell and Ylonen *et al.* 2003), or burrows (Clarke *et al.* 1993), or of localized areas, such as thick vegetation (Cassini 1991), rock taluses (Homes 1991), and cliff faces (Cowlishaw 1997).

Examples of the use of refugia and safer habitats are profuse: open-habitat foraging North American porcupines (*Erethizon dorsatum*) sleep in impenetrable buffalo-berry groves, whereas primate species move to the edge of trees and sleeping ledges (Anderson 1984). Prairie voles (*Microtus ochrogaster*) and meadow voles (*Microtus pennsylvanicus*) construct burrows (East *et al.* 1989) whereas greater snow geese (*Chen caerulescens atlantica)* use the complexity of their wetland habitat to gain protection from the arctic fox (*Alopex lagopus*) (Lecomte *et al.* 2008). Nubian ibex (*Capra ibex nubiana*) use cliff edges (Hochman and Kotler 2007), pied cormorants (*Phalacrocorax varius*) prefer shallow wheatgrass habitats (Wirsing *et al.* 2008), and black-tailed deer (*Odocoileus heminonus columbianus*) seek refuge in tall vegetation (Stankowich and Coss 2007).

In this study I investigated whether seals use the shallow water around Seal Island as a refuge. The "control" conditions are presented by the absence of sharks at the island in summer, in addition to the relative lack of sharks at west coast colonies in both seasons. The null hypothesis was therefore "no difference in the relative use of

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shallow and deep water habitats by seals in winter and summer and at south versus west coast rookeries.

1.3.2. Temporal shifts in activity

The observation that there is a prey risk gradient across time is certainly not unique to Seal Island, and many studies have quantified how prey behaviour relates to variation in temporal predation risk. Some of these include: rodents adjusting their foraging and activity patterns in response to lunar cycle variability in predation risk (e.g. Clarke 1983; Bowers 1988; Wolfe and Summerlin 1989), copepods undertaking diel vertical migrations (Neill 1990, Ramos-Jiliberto and Gonzalez-Olivares 2000), little blue heron (*Florida caerulea*) switching their foraging behaviour to safer times when under intense common black-hawk (*Buteogallus anthracinus*) predation (Caldwell 1986), European perch (*Perca fluviatilis)* adjusting their risk-taking behaviour in response to perceived predation risk (Magnhagen and Borcherding 2007), metamorph cane toads (*Bufo marinus*) exhibiting diurnal activity in response to predatory con-specifics (Pizzatto *et al.* 2008), and plains zebra (*Equus burchelli boehmi*), increasing their use of woodland, rather than grassland habitat at night, in response to increased nocturnal activity and attacks by lion (Fischhoff *et al.* 2007). A theoretical framework within which to interpret temporal variation in predation risk, has, however, only very recently emerged, with the publication of Lima and Bednekoff's (1999) risk allocation hypothesis.

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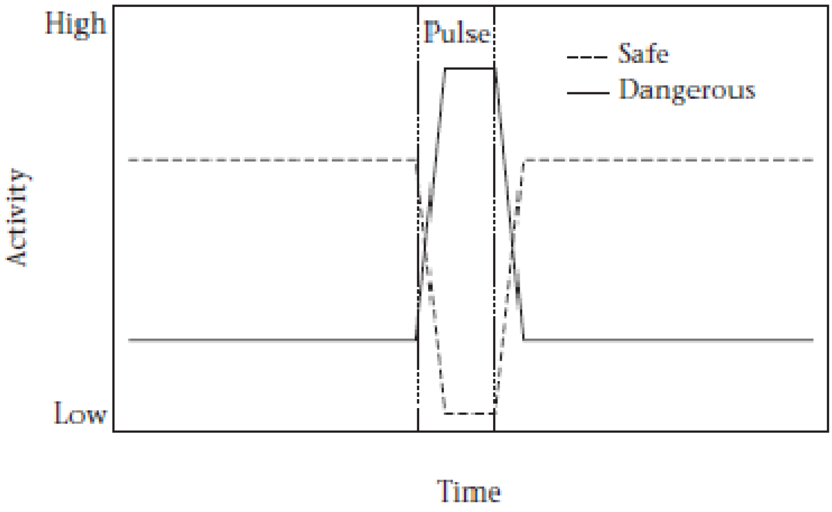

Figure 1.1 Basic predictions of the risk allocation hypothesis (Lima and Bednekoff 1999) as adapted from Sih and McCarthney (2002). Low and high activity respectively, are more likely to occur under brief periods of safety or danger compared to when animals forage under constant risk.

The risk allocation hypothesis (Lima and Bednekoff 1999, figure 1.1.) is based on the idea that animals feeding under temporal variation in the risk of predation face a problem in the optimal allocation of anti-predator behaviour across various states of risk. The hypothesis predicts that during brief, high risk periods, a foraging animal will stop feeding completely and ride out the pulse of high risk in a state of heightened anti-predator behaviour, consequently shifting its feeding activity to a low risk period (Lima and Bednekoff 1999). Several studies have investigated the validity of this hypothesis, but the results have been equivocal: whilst some have found support for the hypothesis in the way that animals adjusted their temporal activities (Sih and McCartney 2002, Eggers *et al.* 2005, Rohr *et al.* 2003, Griffin *et al* 2005.), others have found no evidence that individuals fine-tuned their behaviour, temporally, to risk (Von Buskirk *et al.* 2002, Laurila *et al.* 2004, Koivisto and Pusenius 2003, Sundell *et al.* 2004) and still others have had mixed results (Sih and McCarthney 2002).

One problem that seems to underly these differences is that the artificiality of many experimental systems do not allow for a reliable assessment of the shift in temporal acitivity: Koivisto and Poisinius (2003), Laurila *et al.* (2004) and Sundell *et al.* (2004) all found that animals may habituate to non-lethal experimental cues while other studies (Van Buskirk and Arioli 2002, Koivisto and Poisinius 2003, Sundell *et al.* 2004) found that although prey responded to predators they did not appear to learn the temporal variation in risk. The challenge is thus to find a system where these artifacts are absent, but that still allows an evaluation of this hypothesis.

Seal Island provides just such an opportunity, as shark attacks during winter are concentrated in the hours immediately following sunrise (Martin *et al.* 2005, Laroche *et al.* 2008). In summer and along the west coast of South Africa, shark predation risk is virtually absent. This allows for a quantification of prey movement in relation to

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a short, predictable pulse of predation risk, in contrast to a "control" site and season with which to compare the response.

In keeping with the risk allocation hypothesis, I thus predicted that movement (to and from the island) of seals in the deep water around the island would be low: i) during short pulses of high predation risk during the day in the high predation season (winter), ii) at all times during the high predation season (winter) relative to the low predation season (summer), iii) at south coast islands relative to west coast islands during the high predation season (winter). The null hypothesis was therefore no difference in diel temporal activity by seals during high risk periods in winter (high predation) and no differences between winter (high risk) and summer (low risk) for all times and no difference in the temporal patterns at south coast (high predation) versus west coast (low predation) rookeries.

Of course, the risk allocation hypothesis does not only predict differential activity across time periods of variable risk, but an adjustment in animal behaviour. By performing an initial descriptive search for patterns at Seal Island (chapter 3), I was then able to empirically test this prediction (chapter 4).

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1.4. Reducing encounter and approach

1.4.1. Adaptive behaviours as anti-predator defences

Even when animals cannot adjust their temporal activity patterns (to avoid exposure to predation) they can still alter their behaviour within these patches to reduce detection by predators. Previous investigators at Seal Island have noted less predation onseals in groups versus solitary individuals (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008) but no details on how the seals respond behaviourally to heightened predation risk have been recorded. Within the pinniped family, northern elephant seals (*Mirounga angustirostris*) (Le Boeuf and Croxall 1996) and Australian fur seals (*A.p. doriferus*) (Arnould and Hindell 2001) both species attempt to avoid detection by sharks by diving towards the sea floor at high speed and then hugging the substrate as they swim (benthic hugging). This strategy would appear to be very effective for large phocids, but less so for smaller otariids which have reduced oxygen-holding capacities and thus cannot travel for long before needing to surface.

Clearly there is a need to investigate whether Cape fur seals adjust their behaviour to conceal themselves from sharks. The ability to isolate predator effects on the behaviour of seals was greatly facilitated by being able to observe seals at the same island in both high and low predation periods at both a diel and an annual scale in addition to comparing the behaviour of seals at islands with and without predation.

1.4.2. Group formation

Group formation and size are of particular theoretical importance to the gradient of risk experienced by individuals. Predators are often unable to attack all available individuals in a group (predator swamping, Lloyd and Dybas 1966, Taylor 1976, 1979, Darling 1938), and prey individuals will consequently benefit from a dilution in risk, (the dilution effect -Bertram 1978, Sword *et al.* 2005, Queiroz and Magurran 2005, Garay 2009) and the selfish herd effect (Hamilton 1971, Vine 1971), assuming that the rate at which predators encounter groups compared to single individuals does not exceed this benefit (the encounter-dilution or attack-abatement effect - Turner and Pitcher 1986). Furthermore, prey animals may be more likely to detect an approaching predator (collective detection - Houston *et al.* 1993, Romey 1995, Pays *et al.* 2007), and alert con-specifics (the Trafalgar effect - Foster and Terherne 1981, Godin and Morgan 1985, Houston *et al.* 1993, Pitcher and Parrish 1993, Lima 1995, Hilton *et al.* 1999, Bednekoff and Lima 1998b, Treves 2000), or may be able to reduce their individual vigilance relative to other activities such as foraging, without incurring a greater predation risk (the group size effect - Pulliam 1973, Beaucamp and Ruxton 2008).

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Predators may also find it more difficult to target individuals in a group (the confusion effect - Humphries and Driver 1967, Kitchen 1974, Neill and Cullen 1974, Millinski 1977, Heller and Millinski 1979, Ohguchi 1981, Schradin 2000, Tosh *et al.* 2006, Iannou *et al.* 2008, Ruxton *et al.* 2007), and grouped prey may be able to attack a predator collectively (mobbing - Altmann 1956, Owings and Coss 1977). Colonial breeders such as sea birds and seals may be able to breed synchronously, providing a dilution of risk to vulnerable young (Gross and MacMillan 1981, Patterson 1965, Estes 1976, Robertson 1973). In addition, as a consequence of reduced probability of predation success resulting from one or a combination of group effects, predators may avoid attacking groups when single individuals or smaller groups of prey are available, thus affording a passive, secondary pursuit-deterrent (Caro 1995) benefit to prey (e.g. Garret and Franklin 1988, Fitzgibbon 1990, Van Vuren and Armitage 1994, Alberts and Altmann 1995, Clutton, Brock *et al.* 1999, Olupot and Waser 2001, Haas and Valenzuela 2002, Cresswell and Quinn 2004, Quinn and Cresswell 2006).

Trade-offs to grouping and optimal group size

Despite the clear benefits detailed above, there are also trade-offs associated with being in a group. Individual predation risk may not be diluted if groups are proportionally more likely to be detected by predators than individuals (Cullen 1960, Turner and Pitcher 1986, Mols *et al.* 2003, Iannou and Krause 2008). Furthermore increased competition for mates or food resources (Sansom *et al.* 2008), reduced opportunities to forage (Fitzgibbon 1993) and increased transmission of parasites (Seppaelae *et al.* 2008) are all potential costs that may offset the benefits of group formation.

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Optimal group size

Costs and benefits to group members vary with the size of groups, and these tend to limit observed group sizes to a predictable range, modified in response to ecological factors such as food availability and predation risk (Hoare *et al.* 2004). Within this predictable range, the maximum group size is predicted to be evolutionarily stable where individual fitness equals that of a solitary individual (Brown and Alkon 1990, McNamara and Houston 1992, Rannala and Brown 1994) and the optimum group size is where individual fitness is maximized (Rannala and Brown 1994). The modal observed size is usually somewhere between the optimum and stable group sizes (Giraldeau 1997, William *et al.* 2003, Hoare *et al.* 2004, Sumpter 2006).

Establishing the driver of group size distribution

Although costs and benefits of group size may be important drivers in group size distributions, they are not the only factors that may determine group sizes in animals. One of the great challenges in behavioural ecology is teasing apart variables that influence foraging and predation decisions in free-living animals (Altmann and Altmann 2003). Even though one of the biggest trade-offs of aggregation is increased foraging competition it is often simultaneously one of the biggest advantages of grouping from the perspective of reducing predation risk (Houston *et al.* 1993, Jansen and Goldsmith 1995, Romey 1995, Johnson *et al.* 2002, Roberts 2005, Bohlin and Johnsson 2004, Reluga and Viscido 2005). In a study on elk, a positive association between group size and distance to cover was found (Creel and Winnie 2005), a result the authors suggested was often interpreted as an anti-predator activity. Creel and Winnie (2005), however, subsequently found that herd size increased in this way only on days when their predators (wolves) were absent. On days when wolves were present herd sizes remained much smaller. This finding supports Roberts' (1996) contention that it is almost impossible to tease apart foraging and predation effects where both factors are present.

In addition to the difficulty of teasing apart foraging and predation, it is similarly difficult to tease apart different theories of group formation under predation risk, as many make similar predictions. For example, an individual's "cover" by its fellow group members is not the only advantage to be gained from grouping in the presence of a predator (Parrish *et al.* 1997). Other benefits include coordinated group defence, increased probability of detecting a predator, and a decreasing probability of death by, or encounter of, a predator (Hamner and Parrish 1997, Childress and Lung 2003, Reluga and Viscido 2005).

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The difficulty of teasing apart vigilance and risk dilution

An important advantage of group living is the many eyes effect (Pulliam 1973, Houston *et al.* 1993, Romey 1995). A high predator encounter risk is known to increase the frequency with which an individual scans its environment (Childress and Lung 2003, Houston *et al.* 1993, Bednekoff and Lima 1998b). Vigilance bears a direct relationship to aggregation because animals may rely on fellow group members for early warning of danger (Treves 2000). There are two important pay-offs of vigilance, firstly if detection (by any individual) occurs before a predator is fatally close, all members of the group may escape (Pulliam 1973). Secondly, because more eyes are available for detecting the predator, individuals in larger groups can decrease their contribution to vigilance and increase the time spent on other essential activities such as feeding (Roberts 1996, Bednekoff and Lima 1998*a*, Treves 2000). This relationship has been particularly well studied and many examples, especially in ungulates, have been reported (e.g. Dukas and Clark 1995, Lima 1995, Ritz 1997, Blumstein *et al.* 1999, Fairbanks and Dobson 2007, Planque *et al.* 2006). In pinnipeds, Terhune and Brillant (1996) found that vigilance in harbour seals (*Phoca vitulina*) decreased as the group size increased on the haul-out sites where they were frequently “preyed upon” upon by humans.

The interpretation of selfish herd and dilution effects are often unclear in the literature (Beauchamp 2008). While the individuals in a group certainly experience diminished risk, the original predictions for the dilution effect (Pulliam 1973, Turner and Pitcher 1986) are exactly opposite to those of Hamilton’s (1971) selfish herd hypothesis. The dilution effect predicts an equal numerical dilution of risk in a group while the selfish herd hypothesis predicts different costs to individuals in different positions within the group. Having said that, a major point in the literature is that vigilance and dilution (selfish herd effects or otherwise), are interdependent (Lima and Zollner 1996, Roberts 1996, Fairbanks and Dobson 2007, Beauchamp 2008). As group size increases, vigilance decreases, but reduction of risk through encounter-dilution also occurs (Roberts 1996). In turn, the reduction in predation risk associated with grouping may not come through dilution per se but through the vigilance benefits of large groups deterring predators from attack at a rate proportional to group size (Roberts 1996).

The difficulty in teasing apart cause and effect, has also been noted in experimental studies on group size, where the vigilance-aggregation response could also have been due to dilution (e.g. in sun skink lizards, Downes and Hoefer 2004). Childress and Lung (2003) argued that dilution is more important than vigilance if vigilance is less costly (i.e. when prey isn’t feeding). The reverse has also been noted by Lima and Zollner (1996) where the “break” from scanning the environment allows each individual a greater intake of energy than would be possible in the absence of many eyes.

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When grouping is not functional

Another considereation is that not all emergent properties of a system may have a function: some may simply be pattern (Parrish *et al.* 2002, Parrish and Edelstein-Keshet 1999). Ideal free distribution theory states that aggregations can be the result of individuals assorting uniformly relative to resource availability and quality: high quality patches will end up with dense groups (Fretwell and Lucas 1970, Parrish and Edelstein-Keshet 1999).

Thus, aggregations may arise from simple random encounter (Edelstein-Keshet 2001), and group size subsequently maintained and shaped by the cost and benefits of group membership to individuals (Clark and Mangel 1986, Giraldeau and Gillis 1988 Hoare *et al.* 2004). Optimality theory predicts that the energetic and risk pay-offs to individual group members would shape group size distributions to fall within a predictable, stable range, where the maximum group size is a value where individual fitness equals that of a solitary individual (Brown and Alkon 1990, McNamara and Houston 1992, Rannala and Brown 1994), and the optimum group size is one where individual fitness is maximised (Rannala and Brown 1994).

Observed group sizes, optimal group size and proximate questions about how groups form

I've already mentioned the concept of a stable group size larger than an optimal group size, and that not all patterns of aggregation can be attributed to function. These observations highlight an important point: although it is important to understand the costs and benefits associated with group living to explain observed group sizes, these are not only products of functions, but also proximate consequences of how animals behave to form groups. This in turn depends on factors such as the environment (biotic and abiotic) in which an animal lives (Morrell and James 2008), the information it has available to it (Giraldeau 1997, Dall *et al.* 2005), negative and positive feedback (Bonabeau *et al.* 1997, Sumpter 2006), response threshold (Sumpter 2006) decision making systems in animal societies (Conradt and Roper 2003, 2005), leadership (Reebs 2000), synchronization (Cole 1991) and individual selfishness (Sumpter 2006).

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Proximate group formation has been one of the most popular recent research topics, especially within the fields of self-organization (Couzin *et al.* 2003, Couzin *et al.* 2005, Sumpter 2006) and animal decision making (Conradt and Roper 2003, 2005, 2009, Conradt and List 2009). Yet, despite the obvious importance of marrying the functional ‘why’s’ with the proximate ‘how’s’, a strong division between evolutionary and mechanistic biology still exists (Sumpter 2006).

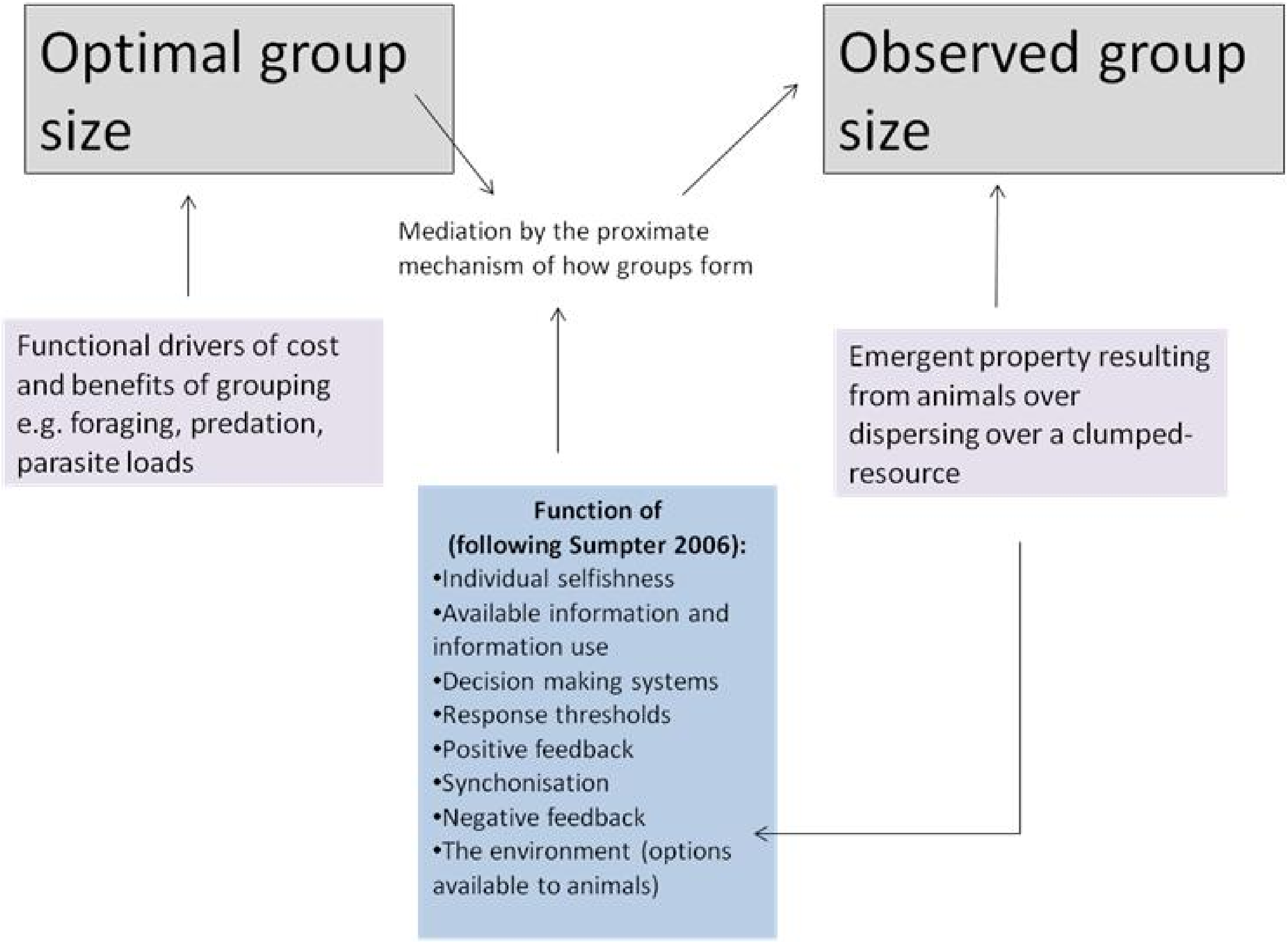

Figure 1.2. Schematic representation of the links between functional drivers of optimal group sizes and the non-functional drivers and proximate factors that result in the different group sizes observed in nature.

The selfish herd hypothesis

An exception to the rule, and perhaps ahead of its' time in this respect, is the selfish herd hypothesis: one of the most popular theories to explain group living within the context of predator avoidance (Hamilton 1971, Barta *et al.* 1997, Dill *et al.* 1997, Romey 1995, Parrish *et al.* 1997 see Viscido 2003 for examples of studies).

In Hamilton's simplest selfish herd model (Hamilton 1971), loosely associated surface-living individuals are preyed upon by a below surface dwelling predator. The predator randomly appears at the surface and attacks the nearest prey individual from the point at which it emerges. Surface-living individuals thus have "domains of danger" - the space around an individual within which it will be the "closest" individual should the predator appear within that space. The larger this area, the greater the individual's predation risk relative to that of its neighbours. By moving towards neighbours an individual can reduce the size of its "domain of danger", which, hypothetically, translates into lower predation risk (Hamilton 1971). Hamilton argued that if all individuals move in this way, compact groups may result.

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Although the selfish herd hypothesis has been cited as an explanation for gregarious behaviour over 600 times (Morton *et al.* 1994) and makes numerous testable predictions about group size and predator targeting behaviour, with much superficial support (e.g., Millinski 1977, Watt and Mock 1987, Fitzgibbon 1990, Uetz 1993, Krause 1994, Watt *et al.* 1997, Krause and Ruxton 2002, Viscido and Wethey 2002, Romey and Wallace 2007), the critical assumptions of the hypothesis have remained collectively untested, owing to several confounding problems in real predator-prey systems (e.g. Pulliam 1973, Fitzgibbon 1990, Uetz 1993, Quinn and Creswell 2006, Romey and Wallace 2007). Predators often avoid selecting more vigilant individuals (Quinn and Creswell 2006), might find individuals in groups more difficult to target (Krause and Ruxton 2002, Caro 2005), might preferentially target prey individuals of different body size (Uetz 1993, Romey and Wallace 2007), experience (Milinski 1977, Uetz 1993, Romey and Wallace 2007), or state of hunger (Milinski 1977, Romey and Wallace 2007).

Consequently, the central prediction that an individuals' spacing affords it differential predation risk has been largely neglected with (to the best of my knowledge) only one study having shown that predators (sparrow hawks) target more widely spaced prey (redshank), relative to non-attacked neighbours whilst controlling for predator confusion, centre/edge positioning and, to some extent, vigilance (Quinn and Cresswell 2006).

Movement rules, as predicted by the hypothesis (individuals move towards the gaps inbetween their two nearest neighbours) have been investigated by a number of computer simulation studies (Viscido *et al.* 2002, Morton *et al.* 1994, Morrell and James 2008). These have revealed another dilemma: simple movement rules, as proposed by Hamilton, do not produce large, compact aggregations, but small mini-herds. More complex rules (animals moving towards multiple neighbours, or applying some averaging decision making) do seem to result in large, dense aggregations, but these may be too complex for animals to follow. However, there has been very little empirical investigation into movement rules in animal aggregations within the context of the selfish herd (but see Morton *et al.* 1994).

What can Seal Island tell us about grouping?

Functional causes of grouping in seals at Seal Island: grouping for food versus predators?

Clear spatial separation of foraging (seals forage far from the island) and predator avoidance (most attacks occur around the island) allow seal behaviour to be interpreted exclusively within the context of predator avoidance. Earlier observations made by Rand (1959) and Gentry *et al.* (1986) that Cape fur seals depart in groups but scatter once they are out at sea seems to suggest that group formation, or congregation formation (Parrish 1991), could indeed be an anti-predatory response, and that a different strategy is employed for optimal foraging. This means that, around Seal Island, foraging and mating can be ruled out as drivers of aggregation.

Different predator-prey theories

Foraging and predation are not the only two variables that can be disentangled at Seal Island. The attack strategy of great white sharks and the foraging strategy of Cape fur seals together provide a unique opportunity to disentangle vigilance from dilution. White sharks are solitarily hunters (Klimley *et al.* 2001, Le Boeuf 2004) and, as previously mentioned, rely greatly on surprise when attacking their pinniped prey

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(Klimley *et al.* 2001, Martin *et al.* 2005). For this reason, sharks attack seals from depth, concealing their presence in the darkness of deeper water. They detect the silhouettes of surface-swimming seals and attack these seals by breaching at high speed (Klimley *et al.* 1996, Klimley *et al.* 2001, Laroche *et al.* 2008). This attack strategy offers an unusual opportunity to test both the ideas on how predators target their prey and the subsequent evolutionary predictions. This is because white sharks will attack artificial seals, or seal decoys, as if they were live seals on account of their silhouettes being sufficiently similar. Not only can exact distances between individual decoys be measured (and survival probability assigned to specific domains of danger), but these can be repeated to test specific predictions of the selfish herd hypothesis. Furthermore, and uniquely amongst predator-prey systems, this study offers a test of the selfish herd hypothesis that effectively controls for prey vigilance.

What about non-functional drivers of aggregation?

Seal Island is two hectares in size, with a population of approximately 77 000 seals during the austal summer (Kirkman *et al.* 2007). The island thus offers a finite, concentrated breeding habitat for seals. The possibility that aggregations of seals in the water may result as an emergent property of aggregations on land can thus not be excluded.

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I argue that, if predation risk alone is driving aggregation, then the removal of predation risk would lead to a disintegration of groups, as individuals would no longer seek to decrease the distance between themselves and their nearest neighbour.To this end, I first quantify the frequency of groups around Seal Island in winter, the peak predation season, and assess their predation risk relative to that of single seals. I then test the prediction that seal groups disintegrate when predation risk is removed by comparing group size distributions at the same site in winter to the safer conditions of summer, and a west coast colony. Having established this baseline, I then investigate these group size distributions and test whether the selfish herd movement rules may be a plausible mechanism to explain group formation and behaviour at Seal Island and hence test the predictions of the selfish herd hypothesis in a natural system.

1.5. The development of anti-predatory behaviour

A last gradient of risk that was defined at Seal Island was the more frequent predation of juveniles compared to adults. In many vertebrate species, juveniles get preyed upon at greater rates and experience lower survivorship than adults (Krause and Godin 1995, Glaudas *et al.* 2006, Hollner and Manser 2006). This may be because of a predatory preference for juveniles (greater probability of successful capture) or because young seals lack the experience to make informed anti-predatory decisions.

Predator recognition and anti-predatory behaviour is greatly influenced by experience in many animals (Griffin *et al.* 2000, 2001, Swaisgood *et al.* 2003, Kelley and Magurran 2003, Ferrari *et al.* 2005, Cameron and du Toit 2005). Even when predator recognition is innate (e.g. Turner *et al.* in press), the correct response to a specific predator (in multi-predator systems) or predatory event must be acquired (Griffin *et al.* 2000, Cook and Mineka 1990). Individuals often learn (observational conditioning, Cook *et al.* 1985) from fearful responses of conspesifics (e.g. alarm cues) to predation events. For example, juvenile rhesus monkeys (*Macaca mulata*) acquire a fear response to snakes after watching adults respond in a fearful way (Cook and Mineka 1990). A similar result was obtained for tammar wallabies *(Macropus eugenii*) in response to a dummy wallaby acting fearfully towards a fox (*Vulpes vulpes*) (Griffin and Evans 2003).

In the less gregarious, more altricial Phocids, physiology often sets the limits for the behavioural development of young (Burns and Castellini 1996, Baker and Donohue 2000, Donohue *et al.* 2000). Although this is less of an issue in otariid species, where neonatal behavioural development is slow enough to be determined by physiological development (*Horning and Trillmich 1997a,b*, 1999, Hochachka 2000), the inability to dive for long periods of time (Fowler *et al.* 2006, McCafferty *et al.* 1998) may seriously compromise the use of diving as an anti-predatory option available to juveniles (Le Boeuf and Croxall 1996).

As encounters with predators can be lethal, and naïve juveniles may have little opportunity to modify their responses to predatory attack, most investigators assume that a genetically predefined predator image that can be modified by learning and

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experience, will be advantageous in situations where cues associated with the predator are highly variable or change over time (Chivers and Smith 1998, Hanson and Cross 2001). Juveniles of Diana monkeys (*Cercopithecus diana*), for example, have been found to be predisposed to use their alarm call repertoire in context-specific ways, but were only able to assemble this into a meaningful sequence given ontogenetic experience (Bshary 2001). Similarly rhesus macaques became fearful of snake images when they were viewed along with adult alarm responses, but not of flower images that were paired with the same alarms (Griffin *et al.* 2002). Latent plasticity to novel cue coupling, via genetic changes or associative learning, could explain many cases of rapid phenotypic change following a sudden shift in the environment (Edgell and Neufeld 2008).

I investigate predation rates on different age classes of seals at the island and ask whether juvenile seals are more frequently attacked because they are preferred to adults, or whether their behaviour simply inceases the probability of exposure to sharks. I also investigate how the behaviour of juveniles changes over the course of an entire high predation season to assess ontogenetic changes that may explain the importance of experience in avoiding exposure to sharks.

1.6. Thesis structure

In this, **Chapter 1,** I have outlined the theoretical rationale for this study in addition to providing a review of the literature relevant to prey behaviour prior to attack, and have identified areas tha require further empirical work which this thesis will attempt to fulfil.

In **Chapter 2,** I introduce and describe the study species (prey and predator) and study sites and outline the general methodology employed in this study.

In **Chapter 3,** I describe patterns of seal activity in relation to defined risk gradients (from previous studies) and observed predatory patterns. After testing the general hypothesis that shark predation affects seal patch use in chapter 3, I subsequently investigate observed patterns in the following three chapters.

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In **Chapter 4,** I test the hypothesis that temporal variation in predation risk influences the temporal patterns of seal activity around the island (the risk allocation hypothesis; Lima and Bednekoff 1999, Sih 2000) and that young of the year acquire anti-predatory behaviour through exposure to predation risk.

In **Chapter 5,** I test the hypothesis that grouping is an anti-predatory response and is achieved by individuals maximizing their survivorship by minimizing their domains of danger (selfish herd hypothesis).

In **Chapter 6,** I test the predictions made by the selfish herd for animal movement within groups and explore some of the problems that have been encountered in in previous investigations.

In **Chapter 7,** I synthesize my results, exploring the extent to which this study has contributed to our understanding of this particular landscape of fear, and our general understanding of predator-prey theory. I outline limitations of the study and detail questions arising from its conclusions.

For the purposes of consistency I have, throughout this thesis, followed Caro (2005) in the use of anti-predatory terminology. In all cases I have used proximate definitions. The scope of this project did not include genetic verification of traits, and data collection was only done over a three year period.

As this investigation is one of proximal (and some ontogenetic) mechanisms, I do not consider the underlying genetics or evolutionary stable strategies. In fact, I refrain from using “strategies” in this thesis.

It is not my intention in this thesis to cover the full scope of anti-predator defences that might be available to seals in relation to sharks, nor to uncover any ultimate causation. Rather I aim to gain insight into our understanding of predator-prey theory by taking advantage of how well intrinsic charachteristics of this system facilitates such investigation.

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While theories provide causal explanations for phenomena and interactions within a particular domain (henceforth referred to as “traits”), the unit by which such a trait is often measured is its adaptiveness. Indeed the association of such a trait with survivorship or reproductive success is often used as proof of causality. Adaptiveness is treated as a unit based on the fundamental principle assumption (Schneider and Wirsing 2008, likens this to a law) that the ecological properties of a species are the result of evolution. To infer evolutionary adaptiveness for a trait demands that the trait should be shown not only to be conferring survivorship and reproductive success now, but also that it has done so in the past. One has to be able to demonstrate that the behavioural trait, or the ability to learn it, is heritable and that there are differences in the gene frequencies that carry this trait within a population (Reeve and Sherman 1993). This is very rarely achieved in ecology. Instead, investigators usually measure the adaptiveness of a trait by (ranked in order of increasing robustness – Caro 2005):

(i) Arguing its adaptiveness – i.e. that a trait is suitably “designed” for a task by virtue of it being shaped by natural selection.
(ii) Inter-specific comparison of traits when a trait is associated with species-related ecological or social factors.
(iii) Correlating traits with reproduction, mortality or lifetime reproductive success.
(iv) Modelling optimum solutions and measuring the fit of these.
(v) Experimentally manipulating traits and comparing mortality or reproductive success with a control sample.

By using these approaches (I use iii to v), a behavioural or morphological trait can only be shown to be adaptive in the weak sense that bearers of the trait will be more likely to survive and hence leave more offspring than individuals that do not bear the trait (Clutton-Brock and Harvey 1977). This is the sense in which I use the word trait in this thesis.

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Chapter 2

General methods

Study sites, study species, data collection and statistical analysis

2.1. Study species

2.1.1. Classification and general biology of pinnipeds

The Cape fur seal belongs to the class Pinnipedia (order Carnivora), which comprises three families: the true seals (*Phocidae*), the walruses (*Odobenidae*), and the earless seals (*Otariidae*). The family *Otariidae* comprises the 14 extant species of fur seals (sub-family *Arctocephalinae*) and sea lions (sub-family *Otariinae*) (Wynen *et al.* 2001, figure 2.1.). The Otariids diverged about 22 million years ago in the early Miocene from *Enaliarctidae* (Repenning 1976), presumably from a bear-like ancestor. The closest extant orders are the *Ursidae* and *Mustaliidae* (Wynen *et al.* 2001).

Physiologically and morphologically, Otariids display remarkable convergence (David 1984, Doidge *et al.* 1986, Kooyman *et al.* 1986, Kooyman and Gentry 1986, Riedman 1990, Pauley *et al.* 2001). Sexual dimorphism is pronounced (Riedman 1990) and harassment from males influences the formation of the mostly temperately situated (Gentry *et al.* 1986), gregarious breeding colonies (Cassini 1999, Cassini *et al.* 2000). Otariids, like all Pinnipeds breed on land (although some Phocids breed on sea ice) and feed offshore on pelagic prey. This has significant implications for lactation strategies (Gentry *et al.* 1986).

A variety of environmental factors, including body size (Burns *et al.* 2004), presence/absence of land-based predators (Schulz and Bowen 2005) and the availability of a stable breeding substrate (Stirling 1975), are thought to have influenced the evolution of species-specific lactation strategies in pinnipeds (Sitrling 1975, Bonner 1994, Boyd 1998). In Otarriids, which are all similar in body size and preferences for breeding substrates, the lactation strategy is closely linked to latitude - a proxy for food availability (Boyd 1998). Otariid species at sub-polar latitudes have access to an abundant food supply for short periods of time, but often have to migrate to find food-rich patches (Gentry *et al.* 1986b). Following a capital provisioning strategy (Burns *et al.* 2004), cows initially invest much energy in their pups that wean quickly and lead a mostly open water existence (Gentry *et al.* 1986a, 1986b, Boyd 1998). Temperate species follow the classic Otrariid income provisioning strategy (Burns 1999) *viz.*, cows intersperse foraging trips with pup

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attendance bouts and administer less lipid-rich milk for a longer period of time. Yearlings typically only wean before the birth of a new pup (Gentry *et al.* 1986, Kooyman and Gentry 1986, Boyd 1998).

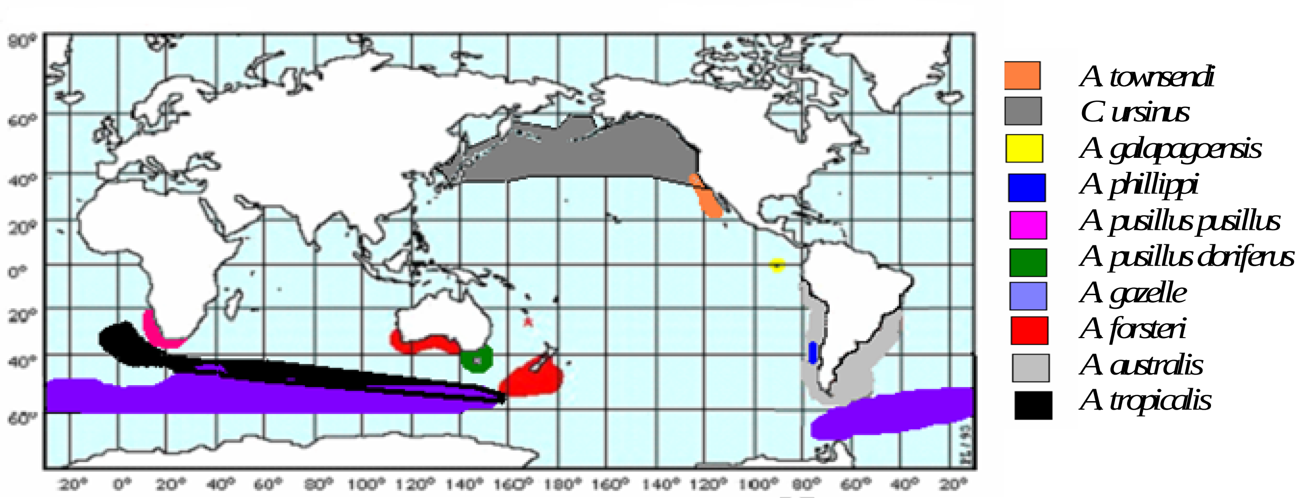

Figure 2.1. Global distribution of the nine species of fur seals (map compiled from FOA distribution maps, *FOA 2006*)

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With the exception of the krill-eating *A. gazella* (Sub-Antarctic fur seal) fur seals occupy a similar ecological role as indiscriminate top carnivores (Pauly *et al.* 1998), preying on a wide variety of teleost fish, cephalopods and crustaceans (Gentry *et al.* 1986b). The availability of these prey species is dependent on upwelling onset (De Bruyn *et al.* 2005), the prevailing wind conditions, degree of coastline depth, width of the continental shelf (Reiter *et al.* 1978) and local transition barriers (frontal zones and bathymetric and sub-marine features that serve to concentrate prey (Stanley *et al.* 2003)). Otariids are preyed upon throughout their distribution by both marine (e.g. killer whales and leopard seals) and, terrestrial predators (e.g. black backed jackals and brown hyenas). All temperate species face a significant predation threat from the great white shark, *Charcaradon carcharias* (Riedman 1990).

2.1.2. The Cape fur seal, *Arctocephalus pusillus pusillus*

Distribution

The Cape fur seal is distributed from Ilha dos Tigres in southern Angola (Meyer 2007) to Black Rock in the Eastern Cape, South Africa. There are 40 recognized breeding colonies (Kirkman *et al.* 2007, figure 2.2.) of which 29 are on rocky islands less than 100 miles offshore and 11 are mainland colonies. Mainland colonies constitute 75% of the total population. The distribution of Cape fur seals have shown a marked shift towards the northern parts of their distribution – 60% of the seal population occurs in Namibia and Angola, of which 60% live north of Walvis Bay, compared to only 20% in the 1980's. The two most Northerly colonies have both formed in the last 10 years (Kirkman *et al.* 2007).

The population of Cape fur seals is thought to have been reduced to fewer than 100 000 individuals, following indiscriminate seal harvesting during the 18th to 20th century (Shaugnessy and Butterworth 1981, Kirkman *et al.* 2007). Since then the population has shown a remarkable recovery: between 1972 (when the first aerial pup-survey was done) and 1993 it was growing at a rate of 3.1%, reaching a total count of around 2 million individuals (Kirkman *et al.* 2007). Although large inter-annual fluctuation in pup recruitment is evident, especially in the northern Benguela which is more prone to environmental fluctuations, the population is thought to have been stable since 1993. The species is considered locally abundant (least concern, Red data list, IUCN 2006), and are considered problem animals in some areas (Yodzis 2001) due to their detrimental interactions with fisheries (Wickens *et al.* 1992, Yodzis 2001) and threatened sea birds (Crawford and Cooper 1996, Marks *et al.* 1997, David *et al.* 2003, Makhado *et al.* 2006). Despite this, periodic population collapses (Matthee *et al.* 2006) have been known to occur, the most recent after a Benguela El nĩno event (Gerber and Hilton 2001)

Threats

As a result of the heavy impact of sealing on Cape fur seal numbers, the population experienced a mild bottleneck prior to the 20th century, in addition to an earlier bottleneck ca. 37 000 and 18 000 years ago, both of which have contributed to a low nucleotide diversity within this species (Matthee *et al.* 2006).

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By far the greatest mortality of Cape fur seals occurs in the pupping season, specifically in the first 50 days after the peak birth date (David 1987a, De Villiers and Roux 1992, Wiesel 2006). Most deaths are attributed to heat stress in new born pups that are unable to swim, and consequently unable to thermoregulate by cooling themselves in the sea adjacent to the rookeries (Wiesel *et al.* 2007). Many of these pups, especially on islands rookeries, drown when they get swept out to sea by large waves (Rand 1969, Francis and Heath 1991, De Villiers and Roux 1992, Wiesel 2006). Females may abandon their pups in times of extreme food shortages (De Villiers and Roux 1992, Wiesel 2006), or a mother-pup bond may fail to establish (McCann 1987).

Other causes of mortality include diseases (Steiger *et al.* 1989), as well as anthropogenic threats such as sealing at Cape Cross-, Wolf- and Atlas Bay colonies in Namibia (a moratorium was put on sealing in South Africa in 1990) (Wickens *et al.* 1992, Yodzis 2000, Yodzis 2001), incidental entanglement in fishing gear and intentional killing by fishermen (Wickens *et al.* 1992).

Colonies south of False Bay are preyed upon heavily by white sharks (Stewardson 1999, Kock and Johnson 2006, Martin *et al.* 2005, Laroche *et al. 2008*), whilst the terrestrial colonies are preyed upon by the brown hyena, *Hyena brunnea* and black-backed jackals, *Canis mesomelas* (Oosthuizen *et al.* 1997, Hiscocks and Perrin 1987, Oosthuizen *et al.* 1997, Nel *et al.* 1997, Wiesel 2006, 2007). Killer whales, *Orcinus orca* may occasionally prey on seals in deeper water (Rand 1959), as may other sharks (Ebert 1991). Sevengill sharks, *Notorynchus cepedianus*, are known to attack cape fur seals throughout the latter's range (Ebert 1991, 1996).

Food

Most of the Cape fur seals' breeding range coincides with the nutrient-rich Benguela upwelling system, one of four major eastern boundary upwelling regions in the world (Shannon and Jarre-Teichmann 1999, see figure 2.2.). Cape fur seals, like most otariids (Reidman 1990, Bonner 1994), can broadly be described as generalist marine predators, preying on a wide diversity of teleost fish and cephalopods (Rand 1959, Shaughnessy 1985, David 1987a, Castley *et al.* 1991, Punt *et al.* 1995,

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Mercenero *et al.* 2006) on the continental shelf, between 10 and 40 nautical miles offshore (David 1987a, Ooshtuizen 1991, Punt *et al.* 1995). Exact diet composition varies in time and across space, but large recorded diet differences between regions have largely been attributed to different fish distributions (Mecenero *et al.* 2006b). Young of the year target different prey species to adults, predominantly hunting crustaceans (small rock lobsters and shrimps) and small teleost fish (Rand 1959). In a refined fish consumption model for lactating Cape fur seal, Mecenero *et al.* (2006a) estimated daily consumption of an average 55kg lactating female at around 11% of her body mass.

Species consumed by Cape fur seals include pilchards (*Sardinops ocellata*), maasbankers (*Tranchurus trachurus*), mackerel (*Scomber japonicus*), snoek (*Thyrsites atun*), cape salmon (*Atractoscion aequidens*), yellowtail (*Seriola lalandii*), mullet (*Liza ramada*), galjoen (*Dichistius capensis*), lanternfish (*Lampanyctodes hectoris)*, pelagic goby (*Sufflogobius bibarbatus),* round herring (*Etrumeus whiteheadi),* red stump nose (*Chrysoblephus gibbiceps*), (Rand 1959, Mercenero 2006 a, b)) and cape hakes (*Merluccius capensis* and, less importantly (David 1987a) *M. paradoxus*) (Punt *et al.* 1995, Mecenero *et al.* 2006 a,b). Seals resident in Namibia feed primarily on juvenile cape hake, cape horse mackerel and pelagic goby, whereas seals living in South African waters appear to eat predominantly anchovy and sardine (David 1987a). Cephalapod species eaten includes Todarodes *angolensis*, *T. eblanae,* Argonauta *argo, Lycoteuthis lorigera,* Ommastrephes *magnificuass, Sepioteuthis australis* (Smale *et al.* 2001, Rand 1959), with *Loligo* species preferred above benthic octopus (Rand 1959).

Life history

Seal colonies vary extensively across seasons in terms of social structure and composition. Adult males arrive in mid-October, where they establish territories and harems at the onset of the breeding season. Bulls do not leave these fiercely defended harems until they have mated with every female (Rand 1963, 1967).

Cows are impregnated almost immediately following the birth of a single pup, although blastocycst implantation is delayed until after the pup is weaned (Rand

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1955, Kooyman and Gentry 1986, Figure 2.2). Pupping itself is a highly synchronized event, with 50% of the colony giving birth within 3 days of each other (Rand 1963, 1967).

Following pupping and mating, male aggression reduces and harems break up (after January). The subsequent period (from February to early April) is characterized by molting (Rand 1956), followed by dispersal of bulls out to sea (Oosthuizen and David 1988). There is much disagreement in the extent to which females are philopatric (King 1983, Wynen *et al.* 2001, Mathee *et al.* 2005), but both sexes disperse as sub-adults (Oosthuizen *et al.* 1991, Wynen *et al.* 2001). Following the departure of bulls from the island, only adult females, some young sub-adult juveniles and pups of both sexes remain at the rookeries during the winter months.

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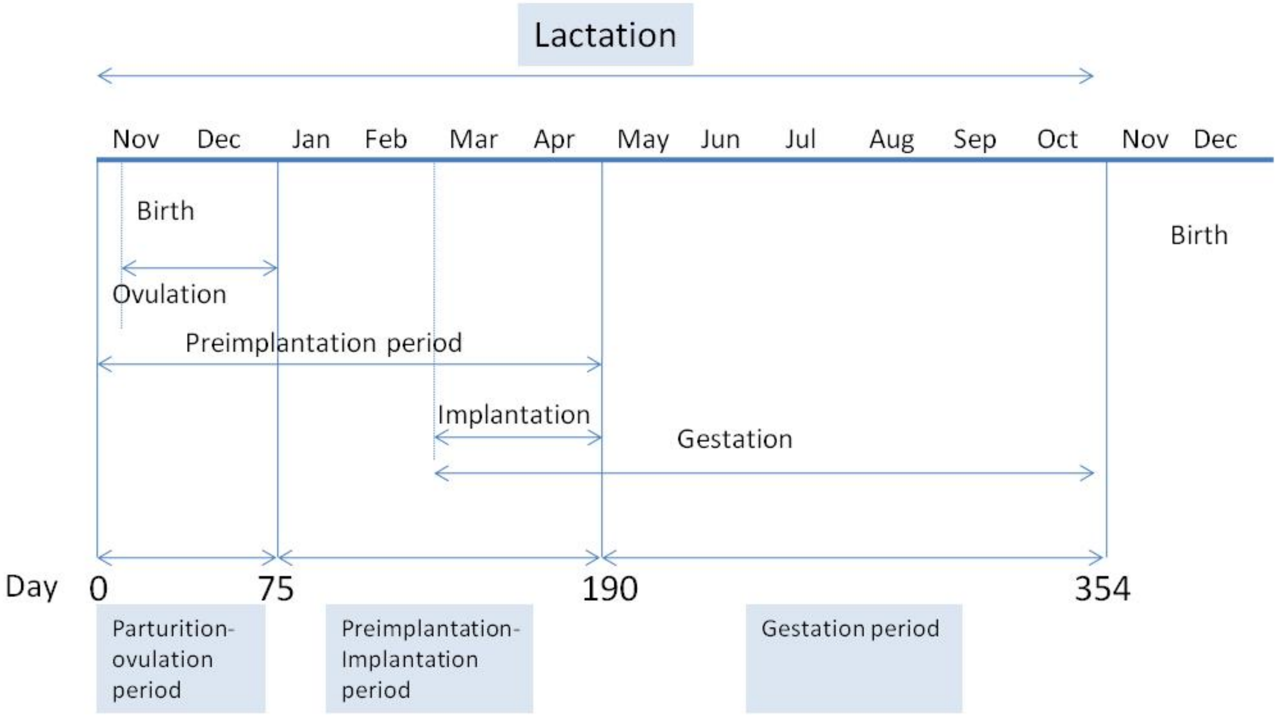

Figure 2.2. Life history schematic of the Cape fur seal (re-drawn from Gamel *et al.* 2005).

In the first few months following birth, initially helpless pups are entirely dependent on cows for survival (Rand 1959, Kooyman and Gentry 1986, Gentry *et al.* 1986). Their movements are therefore restricted, but pups often congregate in “pup pods” while their mothers are at sea (Rand 1969). It can take up to six weeks before they move farther away from the pupping area towards the sea. After this age, they will start spending more time in the shallow water surrounding the rookeries, acquiring swimming, diving and socialising skills (Rand 1959, 1968). Cows intersperse suckling attendance to pups (lasting 3 – 5 days) with foraging trips (5 – 10 days) (Kooyman and Gentry 1986, Gamel *et al.* 2005). It is imperative that cows can recognise their pups' voices before embarking on the first post-birth foraging trip (Charrier *et al.* 2001, Tripovich *et al.* 2008). The occasional failure of first-time mothers to master this and the associated pup starvation, along with mass drowning of uncoordinated pups during summer storms, and heat stress (Rand 1956, 1959, Wiesel 2006), are responsible for high mortalities of pups annually. In a recent study at the Kleinzee colony Gamel *et al.* (2005) found that mothers spend an average of 29.6% of their time ashore and 70.4% at sea. As in all fur seals, feeding trips get longer as weaning approach (Rand 1959, 1967, Gamel *et al.* 2005, Guinet *et al.* 2004).

Even though pups only wean between 8 and 11 months of age (August – November), neonates supplement their diets with crustaceans and teleosts from about 5 months. At this age, young of the year would have learned to swim, acquired adult dentition and their black, non-waterproof pelt would have been replaced with a waterproof olive-grey coat typical of yearling fur (Rand 1959, 1968).

During this ensuing post-moulting, pre-weaning period juveniles undergo an even greater range of physiological (Spence-Bailey *et al.* 2007) and behavioural developmental changes (Reiter 1978, *Horning and Trillmich 1997a,b*, Boyd 1998 McCafferty *et al.* 1998, Rand 1955, 1959, 1967), which serve to enhance their feeding, diving and navigating abilities (Bekoff 1972, Davis *et al.* 1985, Pellis 1992, Harcourt 1991, Hall *et al.* 2001, Lea *et al.* 2001, Spinka *et al.* 2001, Louglin *et al.* 2003, Wilson and Liebsch 2003).

The average mass of seal pups at weaning is 25kg for males and 20kg for females (from 5 and 6kg respectively at birth) (David 1987a). Female seals reach adult size at two years of age (Rand 1969) but usually breed for the first time at an age of four to five years (Shaughnessy 1982, Butterworth *et al.* 1985). Although bulls reach

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sexual maturity at an age of three to four years (Rand 1956), they are usually only able to defend a territory and to successfully breed at an age of 10 to 14 years (David 1987ab). The total lifespan of seals in the wild is unknown, but female seals have reached ages of up to 23 years in captivity (Wickens 1993). Marked sexual dimorphism is evident in adults. Females are, on average, 1.4m long, and weigh around 80kg, whereas an average bull is 2.79m long, and weighs 300kg (Rand 1956, Shaugnessy 1982, Oosthuizen 1991). The sex ratio is slightly male-biased at birth (Rand 1956, Shaugnessy 1982, Oosthuizen 1991).

2.1.3. The great white shark, *Charcarodon carcharias*

Population and distribution

Despite a global distribution, all condichtrytes are confined to ca. 30% of the total oceans, fragmented around sea mouths, ocean ridges and ocean margins (Priede *et al.* 2006). Their absence from the Oceanic abyss is thought to be related to high-energy demands that are unsustainable in extreme oligotrophic conditions (Priede *et al.* 2006). White sharks are wide-ranging pelagic apex predators that are found in oceans off every continent other than Antarctica (Compagno *et al.* 2005, Smith *et al.* 1998, Dudley and Simpfendorfer 2006).

Population size and abundance of white sharks in South Africa, and indeed the world is unknown, but evidence from global hotspots suggests that, compared to other shark species, white shark numbers are low (Kock and Johnson 2006). White sharks are classified as vulnerable by the IUCN (Red data list) and have been protected in South African waters since 1991. South Africa was the first country in the world to afford the white shark protected status (Kock and Johnson 2006).

Although population estimates are lacking, white sharks are known to be prevalent off the south coast of South Africa. Pronounced activity has been recorded at three sites: False Bay, Gansbaai and Mossel bay (Kock and Johnson 2006). Regular movement between these areas have been recorded from tagged sharks (Kock and Johnson 2006), and genetic and satellite tracking results suggest movement of white sharks between South African waters and those of Australia and New Zealand (Pardini *et al.* 2001, Bonfil *et al.* 2005). Despite their large range, a number of

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sharks, particularly mature females, display high site fidelity and have remained resident in an area for a number of months (Kock and Johnson 2006). This is particularly true for False Bay, which also has the greatest proportion of large mature females (Kock and Johnson 2006).

There is much seasonal variability in white shark movement. Whereas they are mostly present near seal colonies during the winter months, they are more frequently observed near the mainland shore in summer. This pattern is not unique to South Africa: Californian sharks have been known to show a similar seasonal activity pattern (Ainsley *et al.* 1985).

Life history

Very little is known about white shark life history. Like most condrichtyes, white sharks are thought to be ovoviviparous. Gestation period, reproductive periodicity and litter sizes are unknown, but it assumed that sharks give birth to 2 – 10 pups, every 2 – 3 years, after a gestation of about 12 months, based on reproductive patterns in chondrichthyans of a similar size (Compagno *et al.* 2005, Smith *et al.* 1998, Dudley and Simpfendorfer 2006).

White sharks are sexually dimorphic as adults with females attaining a length of 4.5 to 5m at sexual maturity (approximately 12 – 14 years old) whilst males are between 3.5m and 4.1m at sexual maturity (9 to 10 years). The maximum length recorded for a white shark is 6.4m, the sex of this individual was not known. Longevity is unknown, but thought to be at least between 23 and 36 years, with one estimation as high as 60 years of age (Compagno *et al.* 2005).

Food

White sharks consume a broad spectrum of prey species (Campagno *et al.* 1997). Pinnipeds and other marine vertebrates are the most common dietary items, but there is also a strong piscivorous component (Estrada *et al.* 2006), with both bony fish and chondrichthyans being consumed (Estrada *et al.* 2006). Other prey items that have been recorded include marine birds and reptiles, larger cephalopods, gastropods and crustaceans (Compagna *et al.* 2007). Additionally, sharks have also been known to scavenge on fisheries offal, fish caught in fishing gear and marine

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mammal carcasses. Although white sharks occasionally attack people, such events are rare (Compagno *et al.* 2005, Kock and Johnson 2006).

2.2. Study sites

2.2.1. Seal Island, False Bay

Seal Island is a granitic outcrop about 2 hectares in area, with a maximum elevation of 6m. Cape fur seals haul out at a few other small rocks in the bay, such as those at Partridge Point near Simon's town (Oosthuizen and David 1988) but Seal Island is the only breeding locality of in False Bay (figure 2.3).. Seal Island is the second largest breeding colony in South Africa in terms of pup production, and the largest colony (between 36 000 and 77, 000 individuals) that is based on an island (Kirkman *et al.* 2007).

Between 1687 and 1800 reports from European visitors suggested an abundance of seals (Shaugnessy 1984, Kirkman 2007b) at Seal Island. However, as a result of uncontrolled harvesting and disturbance from guano collectors (Rand 1952) the population had completely collapsed by 1905 (Kirkman *et al.* 2007). Some legal protection was afforded to seals as a result of the fisheries protection act between 1893 and 1905, and again in 1934, and guano collection ceised by the 1840s. Although not much is known about seal numbers in the first half of the last century, seal numbers had recovered by the 1950s, with more than ca. 2900 pups recorded per annum between 1951 and 1975 (Kirkman 2007b). Controlled sealing continued at the island until 1983, with upper limits to the quota set at 4500 immature seals and 1000 bulls. With the exception of the bull quota in 1982, quotas were never met. The last pup harvest occurred in 1981, and harvesting was officially considered economically non-viable after 1983. Since 1991 a moratorium on seal harvesting has existed in South Africa, and there has been no further harvesting or attempts at hands-on management of the seal population on Seal Island. Between 603 (in 2006) and 8472 (2005) pups were observed in eight years between 1987 and 2006/2007. The seal population at Seal Island appears to have been stable during the last fifty years, except for year to year fluctuations in pup numbers (possibly weather-related), and depressed pup numbers in the 1980's (related to human disturbance) (Kirkman *et al.* 2007).

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The habitat around the island is fairly homogonous with no kelp cover. The underwater topography features a sharp drop off to the north-west, west and south of the Island, whereas a more shallow drop off is evident to the east and north-east. To the south of the Island is an area dubbed the “launch” pad, a shallow outcrop where seals typically aggregate before leaving the island (figure 2.3).

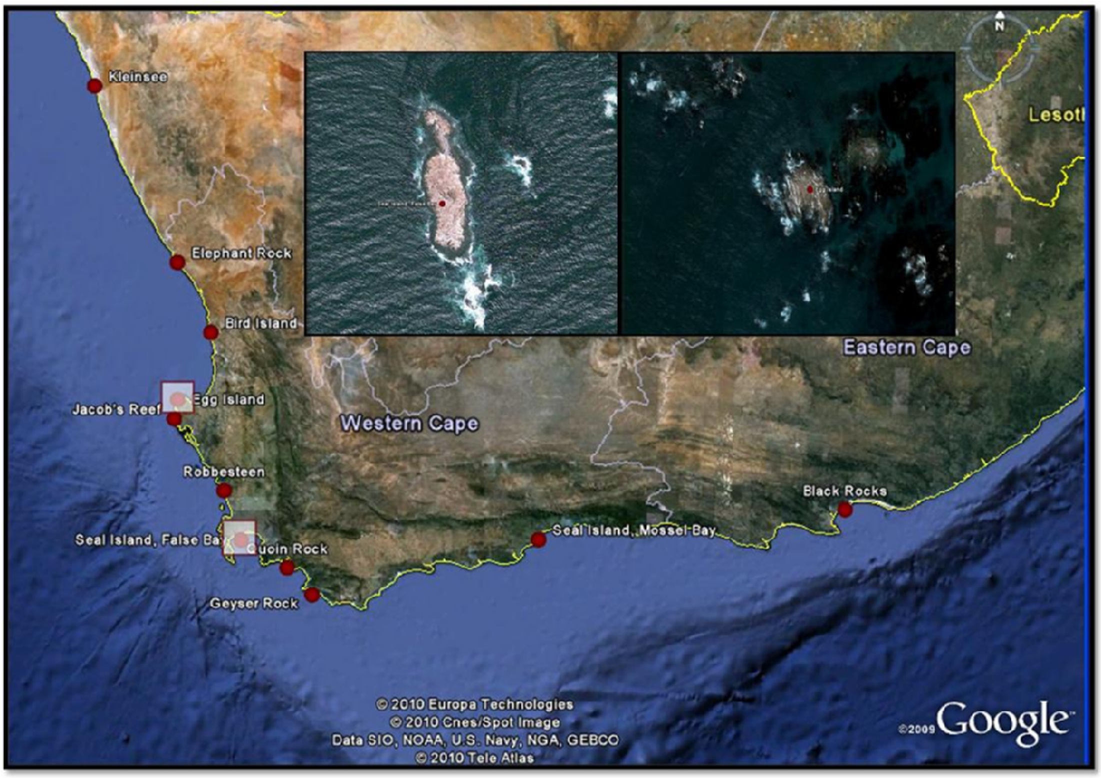

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Figure 2.3. Google Earth image showing the distribution of breeding Cape fur seal colonies (as per Kemper *et al.* 2008). The study sites are indicated with squares, and are shown in the inserts. Seal Island is shown on the left, and Egg Island on the right.

2.2.2. Egg Island (also known as Paternoster Rocks), near St. Helena Bay

Egg Island represents the second largest island-breeding colony in South Africa and combined with the absence of sharks was thus considered to be the most suitable control site to Seal Island. Egg Island, is also a granite outcrop, although much smaller in size than Seal Island. It is situated about 1km to the south of Paternoster, within a sheltered bay. This island has only very recently been colonized by seals. The 1985 pup survey recorded only 5 pups and there are currently between 1000 and 3000 pups which is still substantitally less than the 12 000 – 18000 at Seal Island.

Similar to Seal Island, Egg Island experiences a mild Mediterranean climate, strong prevalent north and south- westerlies in winter and southerlies in summer. The Island is situated close to the nutrient-rich Cape Columbine upwelling cell, and it is thus possible that the seals may have less far to travel to feeding grounds than seals at Seal Island.

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2.3. Data collection and analysis

2.3.1. General data collection

Data collection was specific to distinct questions covered in different chapters, and thus this where I describe them. I refer to chapter 3 for observational sampling, chapter 4 for radio-telemetry data collection, chapter 5 for decoy experiments and chapter 6 for aerial data collection. As different decoy experiments were employed more generally that chapter 5, I describe this below.

2.3.2. Decoy experiments

A prominent feature of shark attacks at the island is its dependence on light (Laroche *et al.* in 2008). Sharks are thought to attack seals at the surface, whilst maintaining the surprise component through concealment in dark deeper water (Ainsley *et al.* 1985, Le Boeuf and Croxall 1996, Klimley *et al.* 1996, 2001). The importance of seal silhouettes in shark attacks is further affirmed by observed patterns of sharks breaching on seal decoys (cut out seal shapes dragged behind a vessel).

I used styrofoam® boards with black ventral surfaces, to construct identical seal decoys which were then fixed into positions on a raft, using lightweight reed poles secured to the dorsal surface of each decoy.

I conducted three different decoy experiments:

(i) To test for the preferred group size targeted by sharks, controlling for direction of travel and vigilance, I dragged a small group of decoys and a single decoy 15m from each other, alternating the formation in front.

(ii) To test shark preference for different age class of seals, I dragged juvenile and adult-sized decoys behind the boat, recording the individual targeted after each trial (n=8).

(iii) To test if the size of a decoys domain of danger is proportional to its relative predation risk, we dragged formation of identical seal decoys around the boat and recorded the targeted individuals. By varying the distances

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between each decoy within a group, I could produce variable and repeatable domains of danger. The use of standardised decoys also allowed me to control for within-group phenotypic attributes. Furthermore, because decoys cannot react to predators I was able to control for prey/group effects such as vigilance and predator confusion. Although this suited a test of the selfish herd hypothesis, the fact that decoys don't react to approaching predators meant that the the

Decoys were towed at a distance of 30m behind a 5 m semi-rigid boat at an approximate speed of 7km.h-1. Both seals and sharks were habituated to the close proximity of motor boats as both tour operators and researchers have used boats to observe shark/seal interactions at the island for more than ten years. I towed decoys through five 1 km long transects on 16 separate days and recorded a total of 36 independent attacks. After each predation event I recorded which decoy had been attacked. Decoys on rafts were designed to break free from the raft upon attack, reducing the chances of injury to the shark and enabling a conclusive assessment of the targeted decoy.

2.3.3. Measures of fitness

This thesis focuses on behaviour prior to attack within the framework of the predator sequence. In cases where I was able to associate attack probability or death with an observed trait, I use this measure to infer relative adaptiveness (in a loose sense, as defined in chapter one) of this trait. This approach assumes that individuals that survive have a higher fitness (number of offspring surviving to reproductive age) than those who do not have this trait.

In experimental cases, where decoys were used, I used attack rate as a measure of the probability of death. In assessing whether movement rules result in reduced or elevated predation risk, I assign predation risk based on the results obtained from decoy experiments. Thus a seal which moves towards other individuals is considered to have reduced predation risk and hence a higher level of fitness relative to an individual that moves further away from other individuals. Finally, for temporal movement decisions and the ontogeny of juvenile behaviour, I use mean shark presence recorded at the

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island at different times of the day and year and the associated predation risk as measures of cost.

2.3.4. Prey selection index

To assess the relative risk associated with different group sizes, age classes or behaviours, I used Jacob's prey selection index (D) (Jacobs 1974). D can be calculated using the formula:

$D=(r-p)/[((r+p) - 2rp)]$

Where r = proportion of prey in the predator's diet
p = proportion of prey in the environment

2.3.5. Statistical analysis

All statistical analyses were conducted using the statistical package Stat Soft. I performed exploratory descriptive statistics prior to running all statistical tests to test relevant assumptions of normality of distributions and homogeneity of variances. Where possible and appropriate I transformed data to meet assumptions of normality and homogeneity of variances using fourth root- (I prioritized homogenizing variances over normalizing data as heterogeneity of variances are particularly difficult to deal with statistically) and arcsine transformations. If data were normal or could be transformed to normality, parametric statistics were used following Keogh and Quinn (2003). In all other cases I used the robust rank-based non-parametric equivalents following Wilcox (2003). 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 2003).

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To analyze two sample datasets I employed student t-tests or the non-parametric Mann-Whitney U when datasets were independent or paired t-tests and non-parametric Wilcoxon paired tests when data points were paired. In instances where a single categorical variable predicted a continuous response variable I employed single factor ANOVAS or either non-parametric 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 I w unable to homogenize variances through transformation, I performed the Brunner-Dette-Mank rank-based ANOVA and calculated standard errors based on the recommended bootstrapping techniques (Wilcox 2003).

For parametric data with a continuous response variable and several categorical predictor variables, I employed 3- and 2- factor fixed factorial ANOVA to test null hypotheses of no differences in means between and amongst factors. To test co-variation between two linear continuous variables, with bivariate normal distributions, I used Pearson's product moment correlation coefficient to test the null hypothesis that $\beta 1=0$.

Where datasets contained both continuous and categorical predictor variables, I employed generalized linear models (GLM) where multiple regressions of random factors did not adhere to these assumptions. Response terms for the GLM analyses were binary and I specified a logit link function (for binomial distributions) to correct for unknown error terms. Estimators were fitted using Grauss-Hermit approximations (as there were very few random effects) and stepwise regression was not required as there was no co-linearity between variables. I use the Wald-F statistic to draw statistical inferences.

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To analyze behavioural frequencies I employed single and multi-level Chi-squared statistics (all sample sizes were such that more than 20% of the variables contained more than five data points). For more complex contingency tables (behaviours at different sites in different seasons), I employed log-linear models to analyze data, using a log function and a poisson error term. I use the log of the odds ratio and the resulting confidence interval to obtain resolution. To analyze group size distributions, I employed Kolmogorov-Smirnoff distribution fitting to test the goodness of fit of group size distributions to normality, and Kolmogorov-Smirnoff 2-sample test to test significant differences between them.

All statistical tests are two-tailed. Parametric means are given with standard errors of the mean and rank-based values of locations with standard errors of the median (Wilcox 2003).

Chapter 3

Spatial behaviour

Does the risk of encountering white sharks influence cape fur seal behaviour around a breeding rookery?

Abstract

Predation is one of the most important drivers of animal behaviour in prey species, but its’ effects are often difficult to entangle from other evolutionary drivers, in particular foraging. At rookeries of marine central place foragers, areas of high predation and preferred foraging are often spatiotemporally separated, allowing a unique opportunity to gain insight into how predator-avoidance shapes the behaviour of prey.. Here I broadly quantify Cape fur seal *Arctocephalus pusillus pusillus* spatiotemporal movement and behaviour in relation to white shark *Charcarodon carcarias* predation risk and ask whether sharks affect the behaviour of seals around Seal Island, False Bay. My results suggest that seals do not adjust their spatial use of the high predation risk area around the island, but that they only use this area when leaving for or returning from the foraging grounds, utilising the safer, shallow area around the island as a refuge at other times. Seals leaving the island showed temporal avoidance of the high risk period immediately following sunrise, but returning seals did not. This behaviour was largely a result of naive young-of-the-year seals returning alone from foraging bouts during peak predation periods. Thus although sharks showed no preference for targeting this age class, these seals constituted the majority of victims as a consequence of this high risk behaviour. Single seals were shown to be at higher risk than seals in groups, and leaving seals did form groups at Seal Island, whilst to a much lesser extent at the low-risk Egg Island.

However, considering that seals still grouped up in summer when risk at Seal Island was low, I conclude that grouping in the deep water zone cannot be attributed solely to predation risk but may also be a consequence of seals over-dispersing at a clumped resource (the island). Nevertheless, predation risk seems to play an important role in shaping group size distributions and the behaviour of seals within groups. Overall, my results suggest that seal behaviour around Seal Island is affected by the risk of being preyed upon by white sharks. The ecological homogeneity of the danger zone, the potential to separate proximate causes of grouping, and an already quantified “landscape of fear” together suggest that the shark-seal interaction at Seal Island would be an excellent predator-prey system in which to empirically evaluate some long-standing ecological hypotheses.

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3.1. Introduction

Prey animals alter their behavioural and morphological phenotypes to offset their vulnerability to predators (Lima and Dill 1990, Lima 1998, 2000, Sih 1998, Heithaus and Dill 2002, Khan and Ghaleb 2003, Werner and Peacor 2003, Schmitz *et al.* 2004, Luttbeg and Kerbey 2005), driving spatial and temporal changes in the frequency and behavioural use of high-risk habitats by prey individuals (Hamilton 1971, Pulliam 1973, Dehn 1990, Lima and Bednekoff 1999, Parrish and Edelstein-Keshet 1999, Caro 2005, Creel *et al.* 2007, Krause 2005, Valeix *et al.* 2009).

Changes in prey behaviour 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). Many pinnipeds forage away from a central place of breeding (Smith and Reichman 1984). Central place foragers may manifest as dense aggregations of individuals on patchily distributed islands in temperate upwelling regions (Boyd 1998, Culik 2001). These aggregations, in turn, represent rich sources of spatially predictable food patches themselves and consequently attract apex marine predators such as a variety of shark species (Golman and Anderson 1999, Heithaus and Dill 2002, Heithaus *et al.* 2009, Laroche *et al.* 2008), leopard seals (*Hydrurga leptonyx*) (Hall-Aspland *et al.* 2004, Ainsley *et al.* 1985) and killer whales (*Orcinus orca*) (Hoelzel 1991).

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Breeding colonies of marine homeotherms offer a much underutilised opportunity to gain insight into how predators affect prey behaviour. In many predator-prey systems, the causes of prey behaviour may be confounded by selective forces other than predation risk. Costs and benefits to an individual's foraging and reproductive success, in particular, may prove difficult to disentangle from behavioural traits that also allow animals to avoid predators (Houston *et al.* 1993, Jansen and Goldsmith 1995, Roberts 1996, 2005, Bohlin and Johnsson 2004, Creel and Winnie 2005).

Marine central place foragers offer an opportunity to control for the confounding effects of reproduction and foraging, as these animals, by definition, forage away from their breeding rookeries, restricting breeding and social behaviours to generally predator-free terrestrial island patches (e.g. Rand 1963, 1969, Gentry *et al.* 1986). Prey behaviour in the comparatively predator-rich "landscapes of fear" (Brown *et al.* 2001) surrounding these rookeries can consequently be accounted for by predation risk alone (although decisions on when to return to the islands will still be affected by foraging needs at sea, and the need to return to the islands to suckle). Seal Island in False Bay, South Africa provides an excellent example of the above scenario. Cape fur seals (*Arctocephalus pusillus pusillus*) experience high levels of predation by white sharks (*Carcharodon carcharias*) in the waters around the island (Kock 2002, Martin *et al.* 2005, Kock and Johnson 2006, Laroche *et al.* 2008). In addition to offering spatial separation of foraging and predation, a number of other intrinsic features make this an ideal predator/prey system in which to study anti-predator behaviour:

Firstly, shark attacks on seals are frequent (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008) and, because sharks typically breach on surface-swimming seals from depth (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008), highly visible. Secondly, predation events are spatiotemporally concentrated, with most attacks happening in the first two hours after sunrise, and within 400m of the southern and western sides of the island (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008). These features allow for a reliable estimate of survival and hence it is possible to assess the fitness costs of different behaviours.

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West coast seal rookeries experience negligible white shark predation (although seven gill shark ranges do overlap with these rookeries, as mentioned in chapter 2), and sharks move away from south coast rookeries in summer (sharks typically depart from Seal Island in October – Kock and Johnson 2006). These spatial patterns, coupled with spatially concentrated predatory activity at Seal Island (Laroche *et al.* 2008) result in the emergence of three distinct seasonal and spatial risk gradients: south coast (dangerous) versus west coast (safe), winter (dangerous) versus summer (safe) and close to island (dangerous) and far from island (safe).

Basic patterns of white shark predation on seals have only recently been quantified (Kock 2002, Martin *et al.* 2005, Kock and Johnson 2006, Laroche *et al.* 2008). Available evidence suggest that sharks largely attack lone juveniles as they return from the foraging grounds (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008). Surprise seems to be very important to the success of sharks: Martin *et al.* (2005) found that more than 70% of attacks lasted less than one minute, and that first time breaches constituted 80%

of all successful attacks (success rates have been reported as 47.3% (Martin *et al.* 2005) and 51% (Kock and Johnson (2006)). Prior to launching these attacks, sharks swim at mid-water column depth (Laroche *et al.* 2008), concentrating their searching activity to the south and west of the rookery (Kock 2002, Martin *et al.* 2005, Laroche *et al.* 2008).

Most breach attacks (Martin *et al.* (2005) reports 87%) are observed in the hours immediately following sunrise (Martin *et al.* 2005, Laroche *et al.* 2008). Light penetration through the water column at sunrise seems to provide the best visual concealment to sharks: sufficient penetration to allow silhouettes to be back lit against Snell's window (Strong 1996), but not deep enough to reveal the presence of a predator to a surface-swimming prey (Laroche *et al.* 2008). The observation that shark success rates drop from more than 55% to less than 40% after 09h00 (Martin *et al.* 2005) offers some support for this idea, and corroborates the importance of surprise (and probably prey vigilance) in this system.

As shark attack patterns have only recently been quantified, it comes as no surprise that seal behaviour in relation to these patterns has received only limited attention (Martin *et al.* 2005, Laroche *et al.* 2008). Martin *et al.* (2005) related spatiotemporal movement of seals to that of sharks based on observations from an ecotourism vessel that focused its attention on shark attacks. Their data show that shark attacks are concentrated in the areas of highest seal availability, i.e. that seals do not adjust their behaviour spatiotemporally to shark risk. Laroche *et al.* (2008), by contrast found that, whilst seals do not adjust their behaviour spatially to sharks, they do temporally. In this study, seals avoided the dangerous morning hours.

Shark attacks are concentrated around the south and west of the island (Martin *et al.* 2005, Laroche *et al.* 2008), which suggests that predation risk is highest in these areas. Optimality theory would predict that seals should avoid these risky patches, unless the costs of doing so outweigh the benefits. The three trophic ideal free distribution model (Sih 1998) predicts that predators should overmatch prey in an area that matches the concentration of the prey's food. Seals do not feed around the south and west of the island (which suggests that an ideal free distribution models doesn't fit this system perfectly), but rather travel through this sector en route to their foraging grounds outside of False bay (Rand 1956, Rand 1959, David & Gentry 1986, also see figure 3.1.). One

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explanation for the high concentration of attacks in this sector could be that sharks "overmatch" a high concentration of prey with the intention of using the shortest mean path to their preferred foraging area. This would need to be investigated more thoroughly.

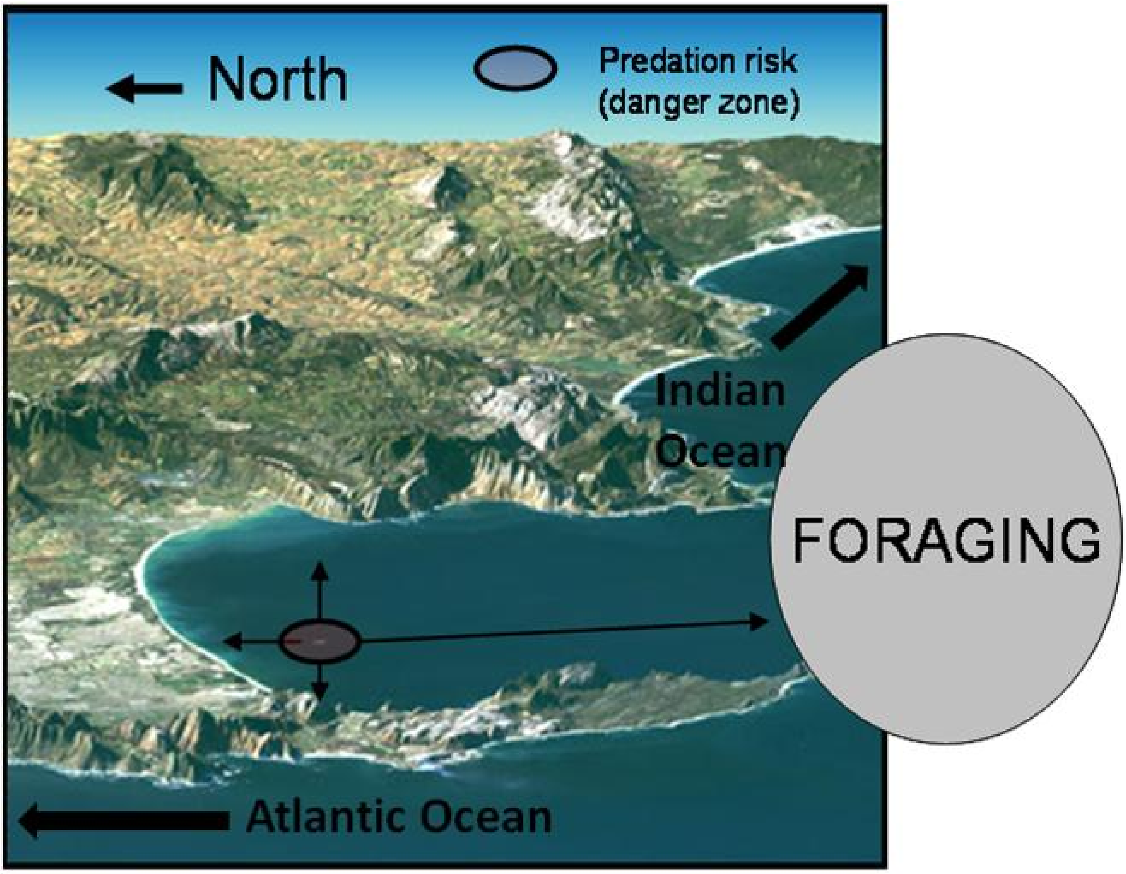

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Figure 3.1. An aerial photograph of Seal Island within False bay including a schematic overlay of the danger zone (red oval area), the four spatial zones around the island, and the preferred foraging area of the seals (image: *NASA Earth Observatory*).

The temporal results are more contentious. The risk allocation hypothesis predicts that prey animals will adjust their activity to predation by reducing foraging activity (or, at Seal Island, foraging-related activity) during high, pulses of risk (Lima and Bednekoff 1999, Sih and McCartney 2002). Given that seals feed mostly at night (Gamel *et al.* 2005) and that predation risk is highly concentrated during brief, predictable time periods, it seems that there is little adaptive value in traversing the danger zone during these hours (although one investigator (Rand 1969) have suggested that early mornings might be the calmest time of day for seals to haul out onto the rookery).

Both studies (Martin *et al.* 2005, Laroche *et al.* 2008) suffered methodological limitations. In Martin *et al.*'s (2005) study, *ad libitum* seal data were collected whilst collecting data on specific seal/shark interactions and shark behaviour around a chumming vessel at the same time. Observer effort was thus not standardized over different days and different periods within day. In Laroche et. al.'s (2008) study, seals were fitted with acoustic tags and their presence at the island recorded by six sub-surface receivers anchored around the 150mx350m rocky outcrop. However the receivers overlapped spatially and did not cover all sectors around the islad and thus it was impossible to unambiguously assign individuals to specific spatial sectors. Additionally, the range of some receivers extended into the danger zone, all so that it was impossible to distinguish seals that were leaving the island from seals that were simply milling in the safe zone.

This safe zone refers to a narrow, shallow area immediately around the island which has been demarcated as safe from predators by both studies (Martin *et al.* 2005, Laroche *et al.* 2008). Although seals are expected to use this area of safety, rather than the adjacent deeper, dangerous water to safely perform non-foraging thermoregulatory (Rand 1963,Kooyman and Gentry 1986) and social (Rand 1963, Reidman 1990) activities, this has not been quantified.

Whilst neither study investigated seal behaviour in the danger zone, it is possible that seals adjust their behaviour in high-risk areas and during high-risk times in the danger zone, even if they do not avoid the use of these patches (Martin *et al.* 2005 suggest that at Seal Island seals do not). One way of adjusting their behaviour is by diving towards the darker water of the ocean bottom to reduce their visibility (Goldman and Anderson 1999, Laroche *et al.* 2008) to sharks. Both elephant seals (*Mirounga leonine*) (Le Boeuf and Croxall 1996) and Australian fur seals (*Arctocephalus pusillus doriferus*) (Arnould and Hindell 2001) dive to avoid detection by sharks and traverse the danger zones at high speed.

Many animals form groups in response to predation. Groups offer a variety of advantages to individuals including predator swamping, risk dilution, improved vigilance though collective detection, predator confusion, a reduction of individual

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vigilance relative to other activities and mobbing (see Magurran and Pitcher 1987, Lima 1998, Ruxton *et al.* 2004, Cresswell 2008, Caro 2005 for reviews).

There is some evidence that seals form groups at Seal Island (Laroche *et al.* 2008, Martin *et al.* 2005, Kock 2002), which, given the absence of other evolutionary drivers of grouping at the island, would be tempting to interpret as having an anti-predatory function, especially given that single seals constitute the majority of shark victims (Martin *et al.* 2005). However, single individuals may be targeted for a number of reasons; including their unique phenotypic attributes (e.g. physiological state, experience) and relative availability. That seals benefit from being in a group through reduced predation risk (either directly or by dilution) has not yet been demonstrated.

I argue that, if predation risk alone is driving aggregation, then the removal of that risk would lead to a disintegration of groups, as individuals would no longer seek to decrease the distance between themselves and their nearest neighbour. If animals are over-dispersing over a clumped resource and aggregations of animals result simply because of many seals being present around a small area, then groups should persist when predation risk is low.

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My aim in this study was to investigate spatiotemporal movement and behavioural adjustment of seals in relation to habitats, times and spaces with high predation risk. I expected:

a. Spatial variation in shark predation to reflect seal availability.

b. Use of the shallow zone as a refuge area, i.e. we expected seals in winter at Seal Island to show less use of the deep water danger zone adjacent to this “refuge” than seals in the safer summer season, and seals at a low-risk island.

c. Depressed temporal activity (number of leaving and returning seals) in relation to predictable periods of high risk in the two hours after sunrise (Lima and Bednekoff 1999).

d. Seals to minimize the time spent in surface waters of the danger zone, by showing increased speed and diving frequency relative to safer patches and the control sites.

e. Seals to benefit from grouping under predation risk, and seals to group in winter (when predation risk is high), but not in summer (when predation risk is low), and not at the low-risk Egg Island.

In addition to these behavioural defences, I also investigated how size class and group size interacted with predation risk given the high frequency of attacks upon single juveniles (Martin *et al.* 2005, Laroche *et al.* 2008).

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3.2. Methods

3.2.1. Study Sites

I collected data for this chapter at Seal Island, False Bay (where there are high levels of shark/seal interaction in winter) and at Egg Island, off Paternoster Rocks (where no seal/shark interactions have been documented). Both study sites are described in more detail in chapter two.

3.2.2. Observational sampling

All observational sampling (*ad libitum* data collection, instantaneous scans, focal follows) was carried out from a 5m semi-rigid inflatable boat stationed at four different positions (north, south, east, and west) around the two study islands (see chapter 2). Daylight hours were divided into four time blocks: after sunrise (07h00–08h29), morning (08h30–10h59), mid-day (11h00–14h59) and afternoon (15h00–17h59). The mid-day and afternoon sessions were extended relative to other time periods as weather conditions often neccecitated returning to land in the afternoons, leaving fewer afternoons than mornings during which data was collected. We thus pooled data to ensure a more balanced sample size.

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Space use around the islands

To assess use of the deep zone and shallow water relative to the island itself, I divided both study sites into three habitats: The deep water zone (water more than 10m from the most exposed part of the islands at low tide, the shallow zone (water less than 5m deep, and between 0 and 10m from the islands' edge), and the island itself. I divided the deep zone into two further zones: a “danger zone” within 1.5km of the island and a “safe zone” more than 1.5km away from each. These zones were charachterised based on previous investigation of spatial predation patterns around the island (A. Kock unpublish. data, pers. comm.), where the investigator took care to quantify shark attacks at different distances from the island, with equal sample effort.

All counts were made using instantaneous scans, taken at 20 minute intervals. Land counts were recorded using a digital camera. Photographs were taken of specific sections of the island using pre-defined landmarks. A manual count of seals observed between two pre-defined landmarks on the land zone was made from each photograph.

Seals in the shallow zone (between the same two landmarks) were estimated by real-time manual counts. By contrast sampling within the deep zone was achieved by recording all seals in the water within the observers' field of vision in a 30 second period. I assumed that my error in estimating seal numbers in this habitat would be similar across sites and seasons. As a measure of habitat use, I 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.

Ad libitum data collection in the deep water zone

All seal activity and attacks in the deep water habitat were recorded *ad libitum*. Seal activity was defined as any swimming movement by seals in the water more than 10m away from the lowest exposed areas of the island at low tide. I also recorded all predatory events associated with specific seal behaviour.

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Seals' behaviour was recorded as either returning (swimming towards the island from a distance of at least 400m) or leaving (swimming away from the island at least 10m from the lowest exposed areas of the island at low tide). In both cases, the number of seals in a group and the size class of all seals was noted. Size classes were assigned as pups (class one, 0-4 months of age), young-of–the-year juveniles (class two, five to eleven months of age), sub-adults (class three, one to three years of age), adult cows (class four), and bulls (class five) (*sensu* Rand 1955, 1959, 1967).

Random subsamples of seals detected in deep water were followed and the behaviour of a focal seal in the group was recorded for 30 seconds. Focals included the following behaviours:

i. Jostling: changing positions within a group of seals by porpoising over or swimming under a neighbouring individual or individuals.

ii. Surface swimming: swimming in a directional manner towards or away from the island, without changing position relative to con-specifics (to distinguish it from jostling).

iii. Diving: submerging with a strong downward directionality without re-appearing within an observer’s scan period.

iv. Evasive manoeuvring (Kock 2002): swimming in a fast zigzag pattern at the surface, combined with high porpoising, sharp turns;

v. Rafting/Milling/Playing: when engaged in any activity that lacks directionality and vigilance.

Seal behaviour and group sizes at Seal Island were only associated with attacks when they were recorded prior to an attack. Attacks were defined as any successful or unsuccessful attempt by a white shark to capture a Cape fur seal. Attacks were detected using the following cues: (a) a shark leaps out of the water (breach), (b) blood or fatty deposits on the water, (c) birds (usually Kelp gulls (*Larus dominicanus*), or sub-antarctic 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 2006, Laroche *et al.* 2008). Attacks were classified as “successful” or “unsuccessful” depending on weather the shark bit the seal or there was evidence of blood/fatty deposits in the water.

Ad libitum data was collected in all zones, in both seasons and at both islands and both inside and outside what corresponds to the danger zone at Seal Island in winter, for a total of 595 field hours.

Focal follows

Ad libitum data were supplemented with focal follows on seals leaving and returning to the island. This data was only collected at Seal Island. Ecotourism operations have been active around this island for more than 10 years, and seals appear well-habituated to the presence of boats. Previous observers have not noted any disturbance of seal groups when following them (Laroche *et al.* 2008), and I am confident that the presence of a research craft did not influence the behaviour of followed seals. I 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 20m from the nearest member of the group to minimize disturbance.

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I recorded the same behaviours as detailed in the *ad libitum* section, in addition to GPS data at 100m intervals while following seals for a maximum distance of 2000m. As most attacks occur within 1000m of the shallow area where seals gather to the south of the island (calibrated as 0m during our follows), we considered seals between 1500m and 2000m distance from the island as representative of activity outside the "danger zone".

In addition to measuring the time focal individuals allocated to pre-defined behaviours, I also recorded the group size and composition of the group it was travelling in, as well as the speed (determined from boat speed) it was travelling at. Boat speed (km/h) was calculated for every 100m, 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. I measured distance as calculated from spatial co-ordinates logged with a Garmin 320 GPS (winter 2005), and a hand-held Gamin e-trex (2006 and 2007 seasons).

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3.2.3. Prey selection index

To assess the relative risk associated with different group sizes, age classes or behaviours, I used Jacob's prey selection index (D) (Jacobs 1974). D can be calculated using the formula:

$D=(r-p)/ [((r+p)-2rp)]$

Where r=proportion of prey in the predator's diet
p=proportion of prey in the environment

I calculated the index based on group numbers present in the habitat, and not individuals.

3.2.4. Statistical analyses

I performed exploratory descriptive statistics as described in chapter 2.

To analyze behavioural frequencies I employed single and multi-level 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 distiributions, I employed Kolmogorov-Smirnoff distribution fitting to test the goodness of fit of group size distributions to normality, and the Kolmogorov-Smirnoff 2-sample test to test for significant differences between them. To control for the large variation in sample sizes and seasons, I randomly sub-sampled within the spatial data set, and compared variables recorded inside the the danger zone with those recorded outside of the danger zone and compared variables between sites and seasons, and between age-classes amongst sites and seasons.

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3.3. Results

3.3.1. Space use around the island

Marked variation was evident in the spatial sector that seals used when leaving from (figure 3.2., Kruskall-Wallis, H=2418.383, p<0.001) and returning (Kruskall-Wallis, H=2331.933, p<0.001) to the island (figure 3.3.). Seals left significantly more from the southern sector of the island (1.06±0.019 groups/hour) 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 significant difference in the number of seals leaving from the western (0.127±0.010 groups/hour), northern (0.158±0.017 groups/hour) or eastern sectors (0.19±0.023 groups/hour) of the island.

Despite the frequency of attacks being higher to the south and west of the island (Figure 3.2.b), these areas were not safer, when controlling for prey availability. 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 north is significantly more dangerous than the southern (z=3.9.06, p<0.001) and western (z=2.262, p<0.05) sectors.

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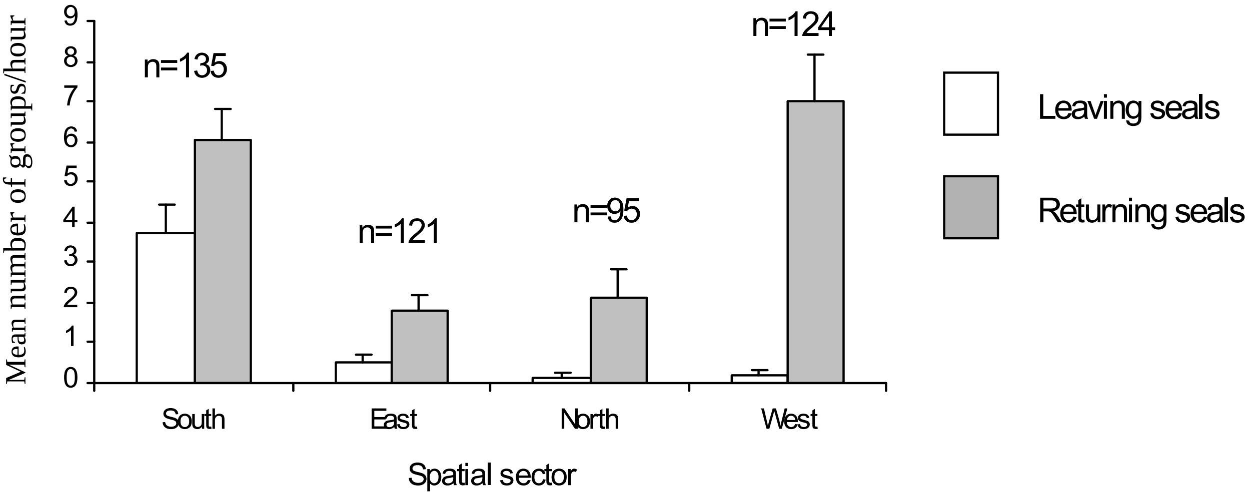

Figure 3.2. (a) Mean number of groups observed leaving (white bars) and returning (grey bars) per hour in different spatial sectors off Seal Island. Error bars represent standard errors at the 95% confidence interval.

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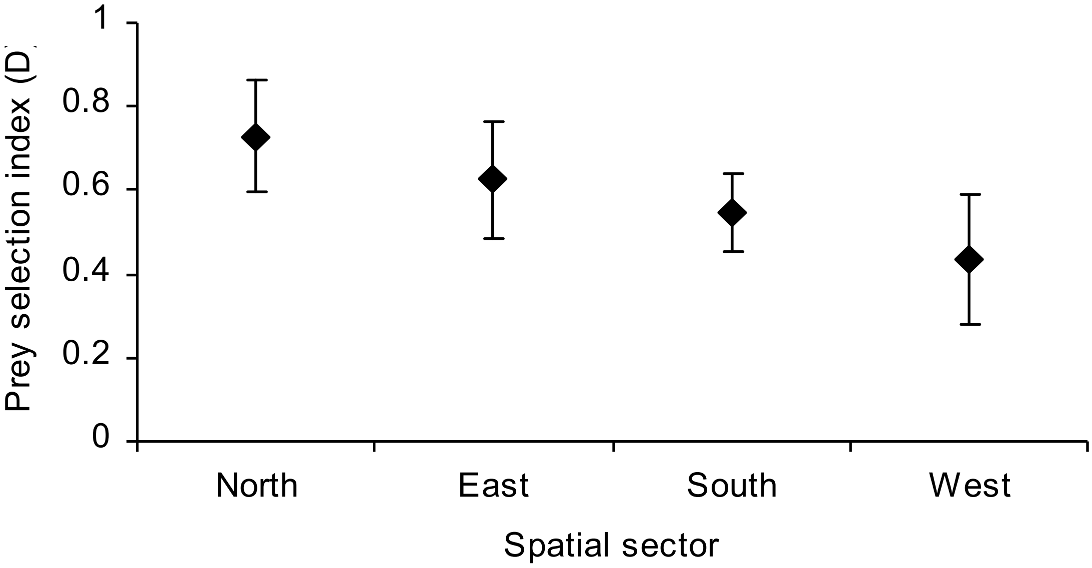

Figure 3.2.(b) Prey selection (measured as Jacob's prey selection index ± s.e. at the 95% confidence interval) in different spatial sectors.

3.3.2. Use of deep water relative to shallow water and land

There was significant variation in the proportion of seals observed in the deep water habitat between seasons and amongst sites (figure 3.3., one-way ANOVA on fourth-root transformed data, F=42.238, p<0.001). The average proportion of seals present in the deep water habitat ("danger zone") was significantly lower at Seal Island in winter (0.063±0.020, n=58) compared to summer (mean=0.76±0.073, n=58) and both seasons at Egg Island (control site) relative to Seal Island (0.650±0.071, n=58 in summer; 0.948±0.036, n=62 in winter). There was no significant difference in deep water use between summer at Seal Island and either season at Egg Island.

3.3.3. Temporal activity of seals

The frequency with which seals returned to the island (figure 3.4.) differed significantly with the time of day. Seals returned to the island more frequently between 07:00 and 08h29 (mean=7.560±1.220 groups/hour, n=319) and between 08h30 and 09h59 (mean= 6.200±1.170 groups/hour, multiple comparison of mean ranks, z=3.780, 2.400, p<0.01, n=299) than between 10h00 and 14h29 (mean=4.4±0.870 groups/hour, multiple comparison of mean ranks, z=5.335, 4.450, p<0.001, n=539) and between 14h30 and 17h00 (mean=1.64±2.14 groups/hour, n=90). Although a relatively larger number of seals were observed to return after dark (mean=5.780±3.9.90 groups per hour, n=26) this was not significantly different to any diurnal time period. Significantly more (multiple comparison of mean ranks, z=5.840, 5.750, 5.510; p<0.0001) seal groups left after dark (mean=22.67±2.312 groups/hour, n=26) than during any of the diurnal time periods. Although a smaller peak rate (mean=2.687±0.659 groups/hour, n=526) was observed between 10h00 and 14h30, this increase was only significant (z=5.840, 4.440, 3.077; p<0.001, 0.001, 0.05) relative to other diurnal time periods (µ=1.650±0.659; 1.6582±0.659; 1.527±1.277 groups/hour, n=319, 320, 85 respectively), when the nocturnal period was excluded (Kruskall-Wallis H=47.864, p<0.001).

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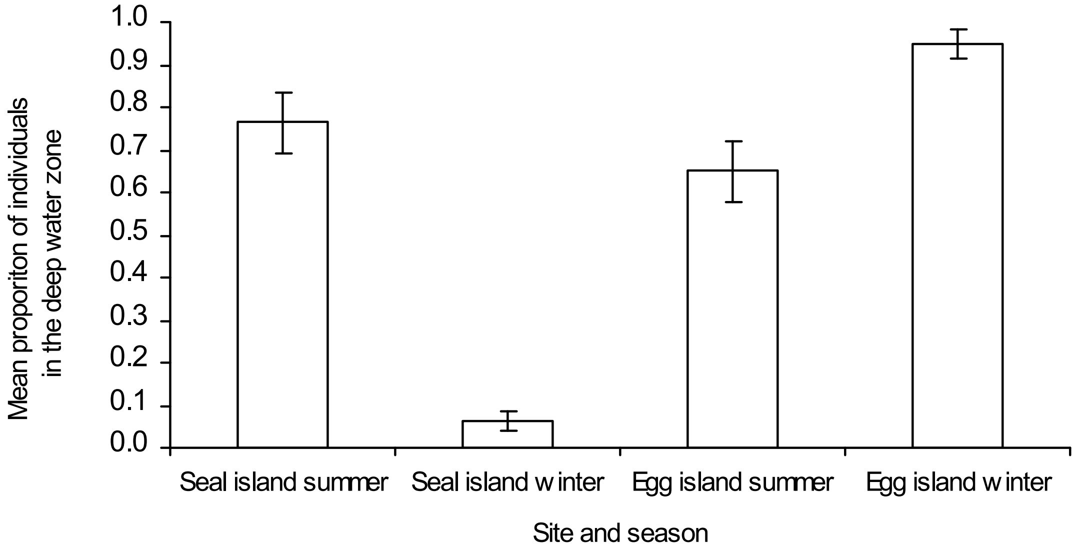

Figure 3.3. Fourth-root transformed values of the mean proportion of seals in the deep water zone, relative to the shallow water and land zones. Error bars represent the standard error at the 95% confidence interval. Data presented is transformed data.

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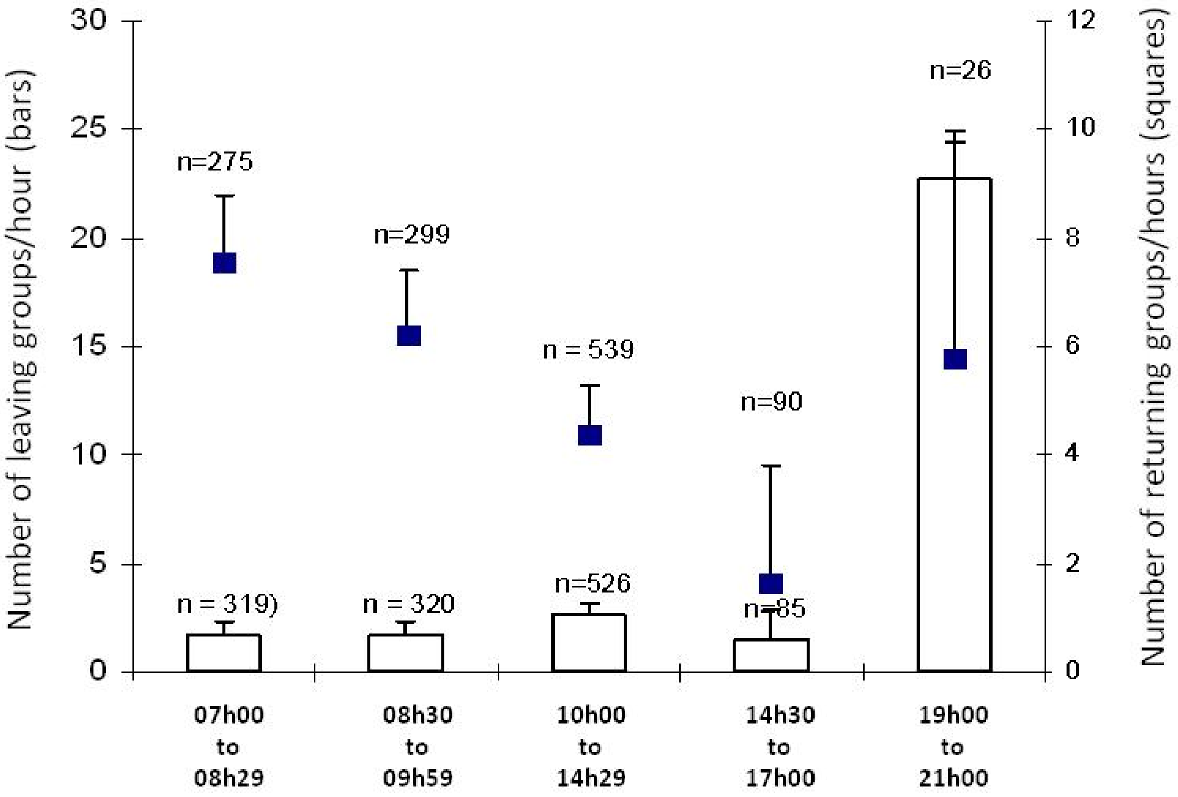

Figure 3.4. Temporal variation in the rate with which seal groups (groups/hour) were recorded leaving from (bars) and returning to (squares) the south side of the island within the high predation risk deep zone.

3.3.4. Seal behaviour at Seal Island within and outside the danger zone in both winter and summer

Jostling

There was significant seasonal and spatial variation in the time leaving seals spent jostling, but no difference for returning seals (figure 3.5.). In winter, leaving seals spent significantly more time jostling (Wilcoxon matched paired t-test, $z=2.599$; $p<0.01$) inside the danger zone (3.7.08±0.740 minutes) than outside (0.800±0.610 minutes). There were no significant differences in the time spent jostling inside compared to outside the danger zone in summer ($n=10$). Seals also spent significantly more time jostling in winter than summer (Kruskall-Wallis, $H=30.586$, $p<0.001$) within the danger zone, but there were no significant seasonal differences outside the danger zone.

Diving

Seals dived significantly more (Wilcoxon matched paired t-test, $z=2.07$, 2.52, $p<0.05$) inside the danger zone compared to outside of it in winter (3.7.5±1.691 minutes inside, 0.833±0.0809 minutes outside danger zone, $n=8$, figure 3.5.) and summer (1.905±1.493 minutes inside, 0.190±0.373 minutes outside, $n=7$). Returning seals dived significantly (Kruskall Wallis, $H=17.820$, $p<0.001$) more than leaving seals inside the danger zone, but not outside of it.

Surface- porpoising

There was significant (Kruskall-Wallis $H=27.090$, $p<0.001$, figure 3.5.) seasonal and spatial variation in the time that returning seals spent surface-porpoising, but not in time spent in this behaviour for leaving seals. Returning seals spent significantly less time surface-porpoising inside the danger zone (2.796±1.315 minutes, $n=8$) than outside the danger zone (Wilcoxon matched paired test, $z=1.95$, $p=0.05$) in winter. There was no significant difference between these habitats in summer (4.315±0.701 minutes).

Milling/rafting

There was significant (Kruskal-Wallis $H=18.950$, $p<0.001$) seasonal and spatial variation in the time that leaving and returning seals spent milling and rafting. Leaving seals spent significantly (multiple comparison of mean ranks, $p<0.05$) less time milling, rafting and playing inside the danger zone during winter (mean=0.127 ± 0.249 minutes, $n=26$) than in summer (mean=1.267 ± 0.790 minutes, $n=10$). There was no significant difference in

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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 (Kruskall-Walls, H=18.950, p<0.001) in winter inside the danger zone (mean=0.074±0.145 minutes, n=9) compared to summer in the same spatial area (mean=1.251±0.798 minutes, 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.

A risk analysis which controls for the proportion of seals engaged in each behaviour at Seal Island in winter (table 3.1.) revealed that seals engaged in surface-swimming (n=76, 38 attakcs), milling/ rafting/playing (n=58, 10 attacks) were selected for 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).

3.3.5. Speed

Seals did not swim at different speeds inside versus outside the danger zone within a season, nor when they were returning to or leaving the island (figure 3.6.). There was however significant variation in 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 seals leaving in winter (predatory season; mean=9.840± 2.052 km/h, n=17), swam significantly faster than returning seals in both winter (6.65±0.828 km/h, n=8; p<0.001) and summer (mean=4.643±1.801 km/hour, n=9; p<0.001), and leaving seals in summer (mean=6.838±2.507 km/h; p<0.0001). No significant differences between any of the other categories were detected.

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Table 3.1. Jacob's prey selection index (ranging from -1 (avoidance) to 1 (selection) by sharks for the different behaviours engaged in by seals at Seal Island in winter.

Behaviour	**D (Jacob's prey selection index)**
Jostling	-1
Milling, Rafting, Playing	0.651090343
Diving	-1
Surface-swimming	0.72972973
Evasive maneuvring	0.153846154

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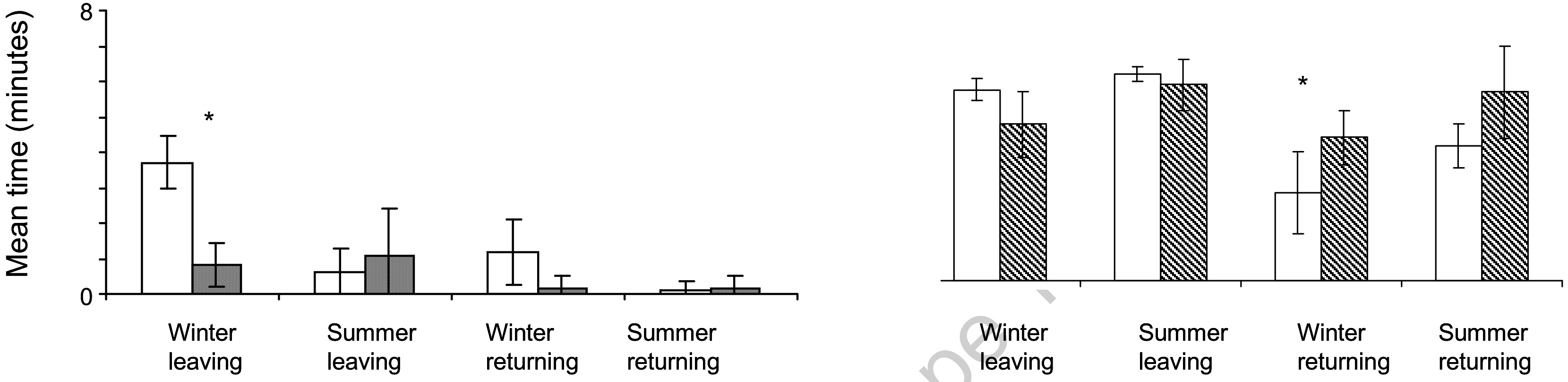
(a) Jostling

(b) Surface Porpoising

(c) Rafting/Milling

(d) Diving

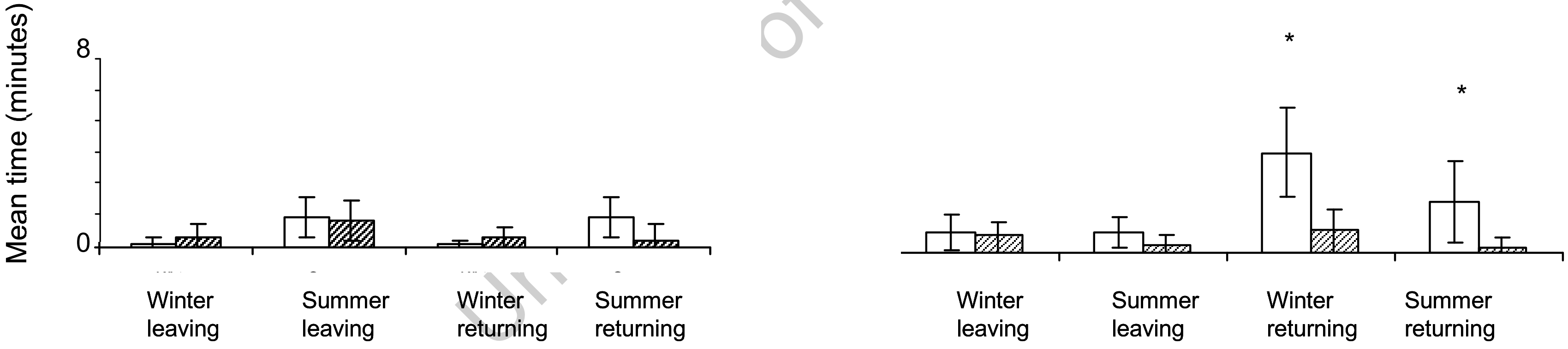

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Figure 3.5. Mean time spent (a) jostling, (b) surface porpoising, (c) rafting/milling, (d) diving by seals in groups inside (white bars) and outside (shaded bars) the “danger zone” in summer and winter when leaving and returning to Seal Island. Error bars represent standard error at the 95% confidence interval. The asterisk (*) denotes statistical significance.

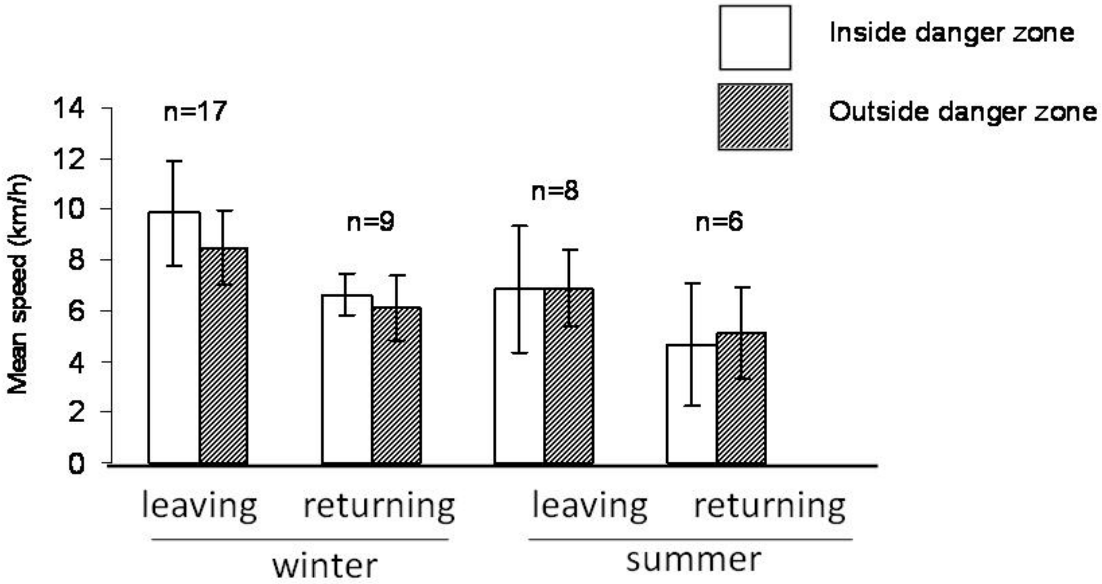

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Figure 3.6. Mean speed (km/h) of leaving and returning seal groups inside (white bars) and outside (shaded bars) the danger zone in winter and summer. Error bars represent standard error at the 95% confidence interval.

3.3.6. Group size

There was significant variation in the median size of groups between study sites, seasons and whether seals were leaving or returning to the island (figure 3.7., Kruskal Wallis non-parametric 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 (EI, n=86); 8±1.359 (SI, n=163) and winter (3±0.823 (EI, n=142); 10±0.478 (SI, randomly sub-sampled n=152 (from 282)). The median size of leaving groups was also significantly ($p<0.001$) larger than returning groups at Seal Island ($p<0.01$ in both summer in winter), but not at Egg Island. There were no significant differences in median sizes of returning groups at either island or in either season.

Group size frequency distributions (figure 3.8.) for returning seals were very similar (Kolmogorov Smirnoff 2-sample tests, $D=0.123–0.193$, $p>0.05$ in all tests) at both islands and in both seasons, with all distributions showing significant left skew and approximating binomial distributions. Group size frequency distributions for leaving seals, by contrast, varied greatly. At Egg Island in both seasons group size frequency distributions were similar to returning group size distributions (Kolmogorov Smirnoff 2-sample tests $D=0.071–0.176$, $p>0.05$ in all tests), they differed significantly from both summer ($D=0.371$, 0.428, $p<0.001$) and winter ($D=0.615$, 0.764, $p<0.001$) distributions at Seal Island. Group size distributions at Seal Island differed significantly ($D= 0.336$, $p<0.001$) between winter and summer, whereas the former approximated a normal distribution, the latter was bimodal. Sample sizes were as indicated in figure 3.7.

Prey selection indices varied significantly for different group sizes (Kruskal-Wallis rank-based ANOVA, $H=70.817$, $p<0.001$). Index values were significantly (multiple comparison of mean ranks, $p<0.001$ in all cases) higher for single (mean $D=0.432±0.056$ s.e.m.) and paired seals (mean $D=0.397±0.097$ s.e.m.) than all larger group sizes. Similarly, selection indices were significantly ($p<0.01$) higher for group sizes of three (mean $D=0.042 ± 0.114$ s.e.m.) and four (mean $D=0.075±0.016$ s.e.m.) than group sizes of five (mean $D=0.00±0.1676$ s.e.m.), six to nine (mean D=-

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0.32±0.193 s.e.m.), ten to fourteen (mean D=-0.25±0.194s.e.m.), and fifteen and larger (mean D=-0.17 ± 0.084s.e.m.). There was no significant difference between any of the group size categories larger than five.

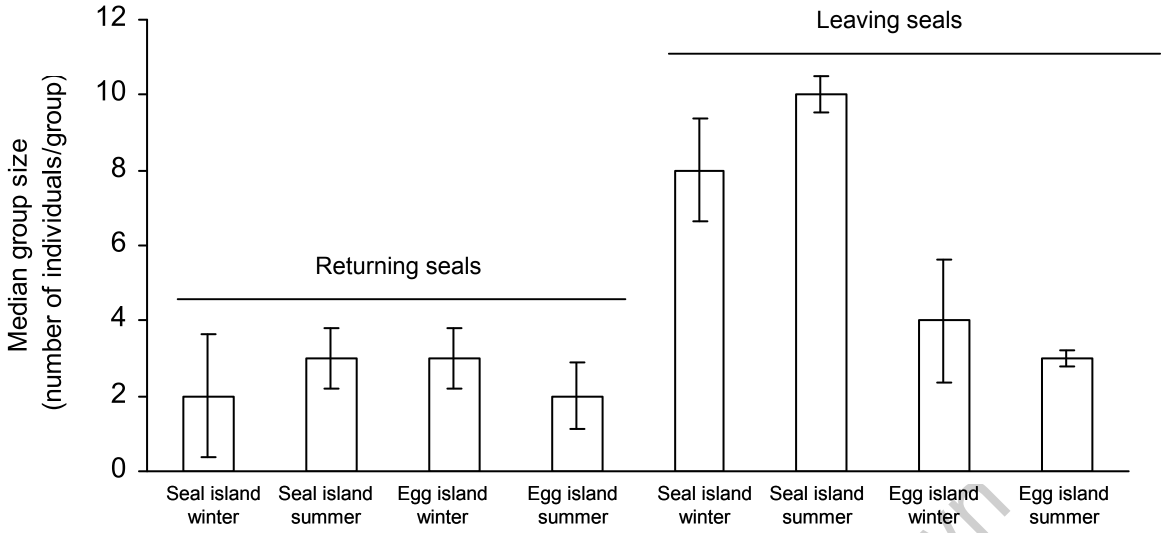

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Figure 3.7. The median size of returning and leaving seal groups in winter and summer at the two different study sites (Seal and Egg Islands). Error bars represent average absolute deviation from the median.

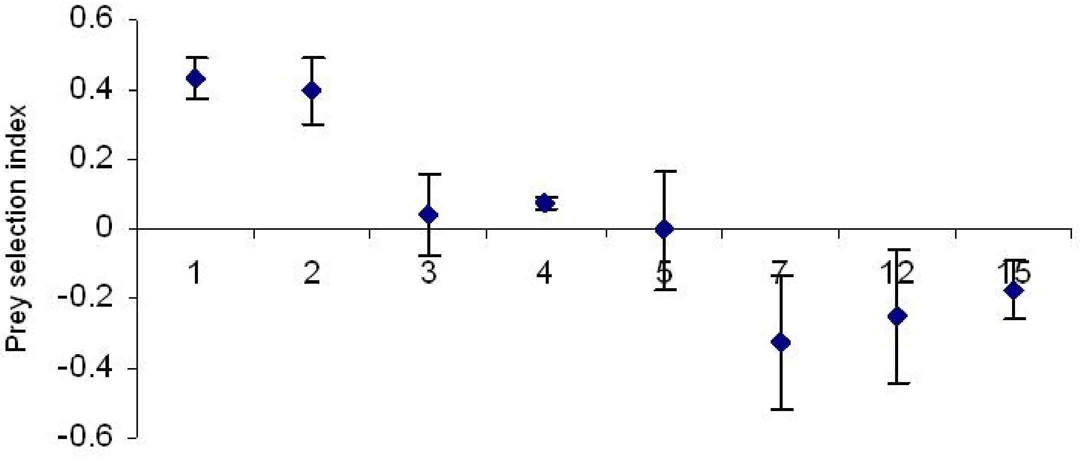
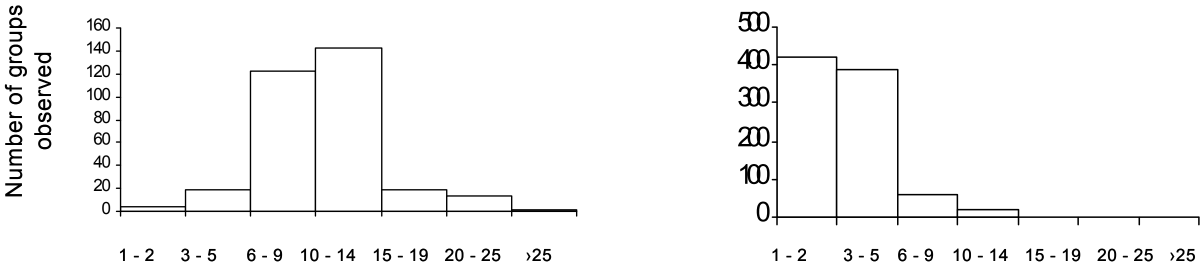
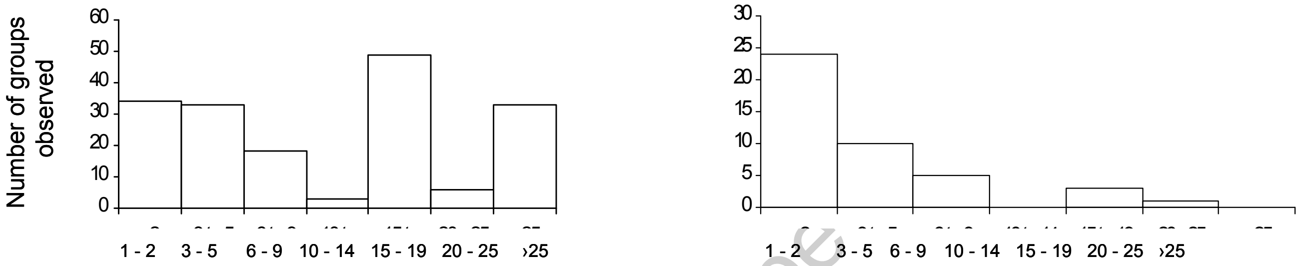


Figure 3.8. Mean prey selection index for different group sizes of seals at Seal Island. Error bars represent standard error at the 95% confidence interval.

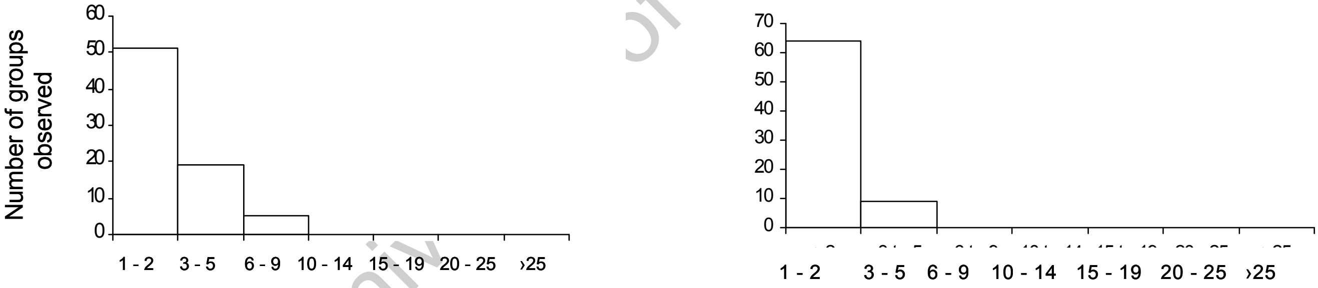
(a) Leaving seals (b) Returning seals



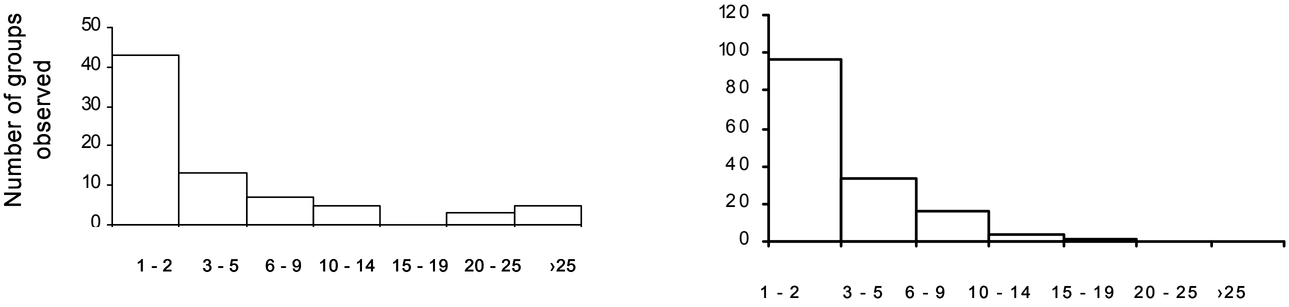
(i) Seal Island winter



(ii) Seal Island summer



(iii) Egg Island winter



(vi) Egg island summer

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Figure 3.9. Frequency distributions of different group sizes for (a) leaving and (b) returning seals at (i) Seal Island in winter, (ii) Seal Island in summer, (iii) Egg Island in winter and (iv) Egg Island in summer.

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3.3.8. Age class and group composition

There were significantly (Chi-squared ^{2}=228.9378, df=3, p<0.001) fewer seals observed leaving the island (n=84) 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.

I found that single individuals and individuals in pairs were significantly (Chi-squared ^{2}=204.556, df=1, p<0.001) more likely to be observed in the danger zone between 7am and 10am than any other group size. I found that these single/paired seals were significantly (Chi-squared ^{2}=139.874, df=, p<0.001) more likely to be juveniles (n=188) than they were to be sub-adults or adults (n=15). I also found that small groups were significantly (Chi-squared ^{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-squared ^{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.

My results show that the seals within the danger zone between 7am and 11am consisted mostly (52.1% of all seals observed) of seals returning alone or in pairs, and small groups (27.6%, Figure 3.10.). Juveniles comprised 74.9% of all single seals, and 86% of all small groups consisted of three juveniles accompanied by one adult seal. Medium (five-nine individuals), large (ten to 14 individuals) and extra-large (more than 14 individuals) groups comprised only 8.3%, 6% and 7.2% of all observed seals.

Juveniles were attacked significantly (Chi-squared ^{2}=10.89, df=1,n=122, p<0.001) more frequently (70.21%) than sub-adults (15.93%) or adult (13.8.7%) seals. There was, however, little difference in the strength of the prey selection index (table 3.2.) between age classes (D=0.088, -0.269, 0.098 for juveniles, sub-adults and adults respectively).

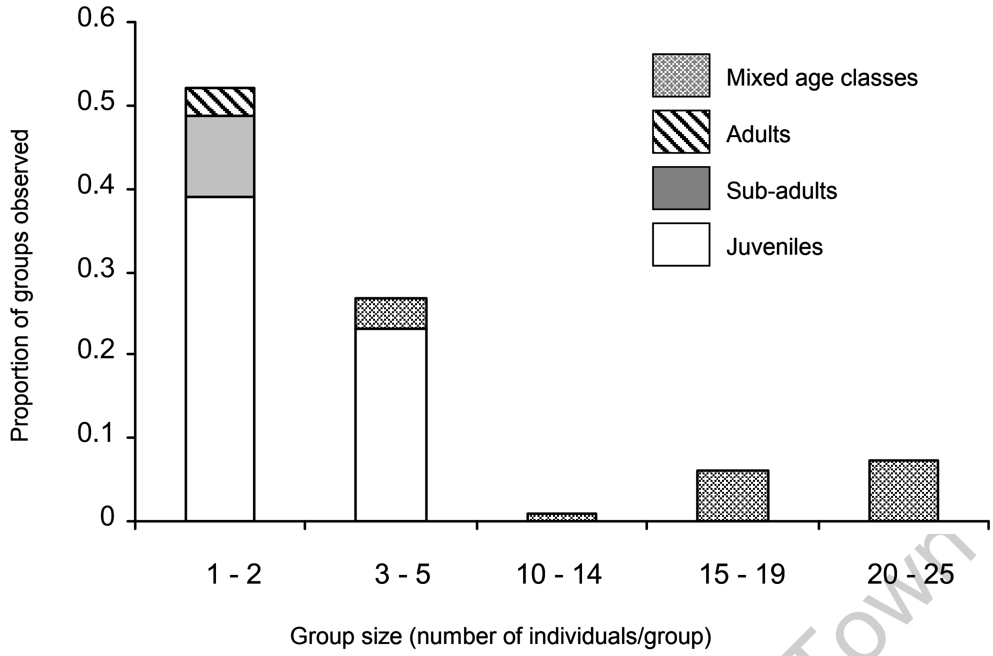

Figure 3.10. Proportion of individuals of different age classes and group sizes observed between 07h00 and 11h00 in the danger zone to the south of Seal Island in winter.

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Table 3.2. Frequency of attacks on different age classes and the corresponding prey selection index (Jacob's prey selection index, D).

Age Class	Frequency of attacks	Prey selection index
Juveniles	86	0.088
Sub-adults	20	-0.269
Adults	17	0.098

3.4. Discussion

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, Sih 1998, Lima 1998, 2000, Heithaus and Dill 2002, Khan and Ghaleb 2003). Spatal adjustment, however, may not benefit prey if both prey and predators are mobile, as predators can simply adjust their behaviour to match the areas of highest prey density.

Spatial variation in seal movement in relation to predation risk

As expected, seals at Seal Island did not appear to modify their spatial patch use around the island to reduce their risk of encountering sharks (figure 3.2.). This may be a consequence of the limited cover around the island and the small area that the sharks have to patrol (see figure 3.1.).

Laroche *et al.* (2008) suggested that the low number of seals moving in predator-diffuse patches 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 (Laroche *et al.* 2008). Whilst I am 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 I show that a trade-off with grouping does not need to be invoked to explain activity patterns, even in departing seals.

Furthermore, seal predation was not higher on the south and western sides of the island, in fact, as seal activity is lower on the eastern- and northern sides of the island in proportion to shark activity; these apparently “safer” zones are actually significantly more dangerous to leaving and returning seals. Additionaly, seals returning from directions other than the south would also have to spend more time in the danger zone, thus exposing themselves to predation risk for longer. It would be of interest to see whether artificial spatial refuges placed in the deep water within the danger zone (e.g. a kelp forest, aritificial rocky outcrop with a shallow patch) would attract seals and hence result in a change in space use to reduce encounters with predators (for examples of

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such experiments see: Hochman and Kotler 2007, Stankowich and Coss 2007, Morgan and Fernández-Juricic 2007).

Although there were no spatial changes in the direction which seals traversed the high predation risk deep waters around the island, they did nevertheless reduce the time they spent within the deep water habitat during winter when sharks were prevalent and attacks frequent. By contrast, seals frequented the “danger zone” during summer months and at the control site (Egg Island) and there was no effect of season on the proportion of seals using the deep water habitat at the control site.

Temporal variation in seal movement in relation to predation risk

Temporal movement patterns reported here corroborate Laroche *et al.*’s (2008) risk adjustment findings and refute Martin *et al.*’s (2005) risk-insensitive findings (figure 3.3.). I show that seals avoided leaving Seal Island during high risk periods, a result that can be explained as temporal adjustment of activity in relation to a short, predictable risk period. This finding supports the risk allocation hypothesis (Lima and Bednekoff 1999). A potential caveat is that seals did not avoid high risk periods upon return to the island, a finding that apparently contradicts Laroche *et al.*’s (2008) finding. However, Laroche *et al.*’s study was focused on adult seals, and closer perusal at the age-class and group-size composition of returning seals shows that returning seals comprised mostly single juveniles (figure 3.8.). Laroche *et al.* (2008) excluded juveniles from their analysis for this very reason, but rather than juveniles being excluded as a confounding variable, they may provide an opportunity to understand the ontogeny of temporal adjustment of activity in fur seals under high predation risk. The risk allocation hypothesis (Lima and Bednekoff 1999) predicts a shift in animal activity under conditions of brief, predictable predation risk. This reasoning appears to explain both my results and that of Laroche *et al.* (2008), but to show empirical support for the hypothesis an adjustment of temporal activity needs to be demonstrated. Considering that context-specificity of predation risk is usually learned (Hanson and Cross 2001, Chivers and Smith 1998, Griffins *et al.* 2002), juveniles provide a good opportunity to investigate a shift in temporal activity through learning.

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Seal behaviour in relation to predation risk

Three broad patterns emerged from my results on seal behaviour within, compared to outside the danger zone across seasons and study sites. First, was the absence of non-directional behaviour (e.g. rafting, milling and playing) recorded at Seal Island during winter (Figure 3.4., table 3.1.) relative to summer and Egg Island in both seasons. Second was the large discrepancy in the behaviour, group size and age class composition of leaving and returning seals (Figures 3.4., 3.5., 3.7.) at Seal Island in winter, and third was the difference in group size distribution of seals leaving Seal Island in winter compared to summer at the control site in both seasons (Figure 3.8.). I will consider each of these patterns in turn.

Rafting, milling and play behaviours were largely restricted to the shallow, safe waters around Seal Island during the high predation winter months but were performed in the deep water (the danger zone) during the low predation summer months and in both seasons at the control site (Egg Island) which has negligible predation in both seasons. Thus seals avoid spending time in the danger zone at times when predation risk is high and restrict the performance of social and thermoregulatory behaviours at such times to the apron of shallow, safe water around Seal Island.

It should be noted that the comparison of Seal Island and Egg Island is not a perfect one, and the validity of the results should be cautiously interpreted in view of the limitations of this comparison. Seal Island hosts a much larger colony (*ca.* 77 000 seals vs. *ca.* 3000 seals) than Egg Island, and no kelp exists around the island, compared to large kelp beds at Egg Island. Kelp may provide a refuge against predators, and provides a habitat to crustaceans which are fed on by juvenile seals (Rand 1955, 1967). Furthermore, the topography of Seal Island is very different from Egg Island. Whereas the former sees a sharp drop-off to the west and south, the latter drops off more gradually, so that the “shallow zone” at Egg Island was a much larger area than at Seal Island.

The observed differences in the group size and behaviour of leaving and retuning seals may be explained in part by life history and foraging patterns. Seals feed far from the island on trips lasting several days and thus lactating females have to intersperse

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foraging trips with attendance bouts. In the Cape fur seal foraging trips and attendance bouts are approximately two to five days in duration (David *et al.* 1986, Gamel *et al.* 2005). Departing seals gather at the launch pad to the South of the Island and typically leave in large (median=8±1.359) groups. However once at sea, seals appear to forage alone (Rand 1959, 1963, David *et al.* 1986), perhaps to reduce competion for limited food resources (Yodzis 2000). As a consequence of foraging alone and without a safe gathering site en route back to the island, most returning seals traverse the deep water near the island (the danger zone) either in small groups or alone.

Seals leaving the island have two anti-predator options: they can either join a group and traverse the danger zone at the surface, or travel alone whilst diving hugging the substrate to avoid detection. There is probably a trade-off between these strategies (Laroche *et al.* 2008), as diving seals are slower and less energetically efficient than surface swimming seals, while surface seals in groups are more visible to sharks. 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). Even if a 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 seals that dive relative to returning seals suggests that traversing the danger zone in a group is more beneficial defence (chapter 5) than diving and that seals only perform the latter when they return as it is not possible safely form large groups.

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It was not possible to validate diving as a direct response to predation risk in returning seals: while seals did dive more inside the danger zone than outside of it during winter, a similar pattern was evident in summer and at the control island. This suggests that diving is not necessarily predator-driven and may be employed for some as yet unkown reason by seals returning to an island.

Another clear behavioural difference between leaving and returning seals was the extensive use of jostling by leaving seals. Jostling is characterized by seals constantly changing positions relative to one another when travelling 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.

One of the aims of this chapter was to establish whether predation risk alone could explain the formation of groups at Seal Island. I argued that if predation was driving group formation then by removing the predation risk seals should no longer group up. The presence of groups at Egg Island in the absence of white shark predation risk (it should be noted that we did not have good information on non-white shark predators for this study, and that this factor might limit the conclusion we can draw from this comparison) suggests that predation risk is not the causative driver of group formation in cape fur seals.

There is however some suggestion that predation may influence the size and structure of seal groups leaving Seal Island. Whereas group size distributions in summer at Seal Island do not deviate from randomness, group size distributions at Seal Island in winter approach normality (figure 3.9.). Specifically, there is a virtual absence of seals leaving by themselves, or in small groups during winter, but not during summer. Group sizes seem to be limited to less than 20 individuals in winter, whilst this was not the case in summer. Furthermore, qualitative scoring of group size compactness during follows revealed that groups in winter were significantly more compact than during summer, although more robust results are needed to corroborate this statement. In short, it appears that seal groups are loosely spaced and form randomly in summer, whilst they are compact and forced towards a normal distribution in winter. By contrast there was no deviation from randomness in group size distribution at Egg Island in either season.

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One theoretical explanation that may be invoked to explain my results on both the behaviour of seals in the danger zone (i.e., jostling within groups) and differences in group size distribution in relation to predation risk is the selfish herd hypothesis (Hamilton 1971). The selfish herd hypothesis is an individual-based model that explains how compact groups could have evolved in previously loosely spaced seal individuals. In a selfish herd model a predator attacks prey individuals at random, targeting the nearest prey individual from where it appears by surprise within a group. Thus unequal predation risk results from differential spacing amongst prey individuals and each group member has a domain of danger around it that can be reduced simply by moving towards neighbouring prey individuals. If all animals follow this movement pattern, the hypothesis argues, compact groups should result (Hamilton 1971).

One explanation for the observed “jostling” behaviour, performed by seals in groups within the danger zone, is that individual seals are attempting to reduce their domains of danger and hence their risk of predation. While the results presented here do not provide direct evidence to support or refute Hamilton’s hypothesis, they do suggest that Seal Island may be an appropriate system within which to test the predictions, especially given the importance of surprise (i.e. no prior directional information of predator position to prey individuals) to the overall success of predation attempts (Martin *et al.* 2005, Laroche *et al.* 2008).

Whereas my study controlled for some of the problems experienced by previous studies, it had limitations of its own. Firstly, I could not collect much data at night, when seal movement peaked (Laroche *et al.* 2008, figure 3.2.) due to the logistical difficulties and dangers of working on a small boat in the dark. Secondly, because I was not working with individually recognisable animals my data are affected by pseudoreplication. Lastly, I could not account for any sub-surface seal movement and thus underestimated the importance of this behaviour in avoiding detection by sharks. These limitations should be addressed in future studies.

Overall, the results presented in this chapter suggest that seal behaviour around Seal Island is affected by the risk of being preyed upon upon by white sharks. Seals modified their temporal use of the dangerous patch of deep water around the island and altered their behaviour in response to predation risk. The ecological homogeneity of the danger zone, the potential to separate proximate causes of grouping, and an already quantified “landscape of fear” together suggest that the shark-seal interaction at Seal Island would be an excellent predator-prey system in which to empirically evaluate prominent theories in behavioural ecology, specifically the selfish herd hypothesis.

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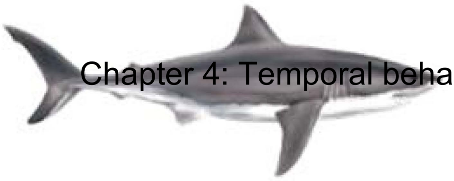

Chapter 4

Temporal behaviour

Temporal variation in predation risk at a seal rookery: a test of the risk allocation hypothesis

Abstract

The risk allocation hypothesis considers the temporal variability of risk inherent in many systems, and predicts how anti-predator behaviour should vary as a function of the frequency and length of risk periods. The major predictions of this hypothesis – that animals should ride out the pulse of predation during brief, risky periods interspersed with long periods of safety, but should prioritize feeding in the compliment scenario – have been tested in many systems, but the results are equivocal. One reason for this may be that the artificiality of many of these experimental systems does not allow for a reliable assessment of the shift in activity as predicted by the hypothesis. Seal Island, South Africa provides an opportunity to address this challenge, because it is a natural predator-prey system with marked diurnal and seasonal variation in both the duration and intensity of predation risk. I found that adult Cape fur seals (*Arctocpehalus pusillus pusillus*) avoided traversing the 'danger zone' where they are at risk of predation by white sharks (*Charcarodon carcarias)* during the high risk period (07h00-09:59) in the season of high risk (winter), but not during the low risk season (summer). By contrast, adult seals at an island where predation risk was consistently low showed no temporal discretion in either season. Furthermore, whereas juvenile seals showed no temporal discretion upon first traversing the 'danger zone', they learned temporal discretion at the predator rich Seal Island, but not at the low-risk Egg Island. Our results provide evidence in support of the risk allocation hypothesis within a natural system by demonstrating that both experienced and naïve seals adjust their activity in response to brief, high risk periods of shark predation.

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4.1. Introduction

Many studies have attempted to understand how prey animals balance activities such as feeding and mating with predator avoidance (reviews in Lima and Dill 1990, Lima 1998, Tollrian and Harvell 1999, Caro 2005, Cresswell 2008), mostly by assessing the behavioural changes of prey in response to the presence or absence of predators. However, temporal risk aversion has been reported in a diverse array of taxa including mammals (Clarke 1983; Bowers 1988; Wolfe and Summerlin 1989), invertebrates (Ramos-Jiliberto and Gonzalez-Olivares 2000, Skutelsky 1996), birds (Caldwell 1986, Magnhagen and Borcherding 2007, Roth and Lima 2007), reptiles (Rohr *et al.* 2003), fish (Fraser *et al.* 2006) and amphibians (Pizzatto *et al.* 2008), and predation risk has been shown to vary with lunar cycles (Clarke 1983; Bowers 1988; Wolfe and Summerlin 1989), season (Griffin *et al.* 2005) and time of day (Caldwell 1986, Ramos-Jiliberto and Gonzalez-Olivares 2000, Pizzatto *et al.* 2008)..

Despite much evidence for temporal risk aversion in prey animals, behavioural ecologists have only recently become interested in how variation in predation risk across time affects individual prey behaviour. Helfman (1989) pioneered this interest by proposing the threat-sensitive avoidance hypothesis, in which prey are predicted to respond to predation risk with an intensity that matches the risk posed by a predator in systems where risk varies temporally.

More recently Lima and Bednekoff (1999) refined Helfman's hypothesis and proposed the risk allocation hypothesis. This hypothesis is based on the idea that animals feeding under temporal variation in predation risk face the challenge of optimal allocation of anti-predator behaviour across various states of risk and predicts that animal activity and anti-predator behaviour should vary as a function of the frequency, length and, in an extension to the model (Ferrari *et al.* 2008b), predictability of high risk periods. Feeding effort is predicted to be lowest during short periods of high risk when these are interspersed with longer periods of safety. Similarly, if long periods of high risk are interspersed with brief periods of safety, animals are predicted to show elevated feeding effort in these short, safe periods. When risky periods are unpredictable, and last longer, however, animals are forced to forage during-high risk situations to meet their energy demands.

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Several studies have subsequently investigated these predictions, but the results are equivocal. Evidence in support of the hypothesis emanates from studies on cover-habitat used and total foraging activity in relation to moon phase by snowshoe hares (*Lepus americanus erxleben)* (Griffin *et al.* 2005), increased movement of elk (*Cervus elaphus*) during periods of safety from wolf (*Canis lupus*) predation (Creel *et al.* 2007, 2008), and decreased use of riskier, but more food-profitable patches by bottlenose dolphins (*Tursiops s*p.), harbour seals (*Phoca vitulina*) and dugongs (*Dugong dugong*) in relation to unpredictable shark predation (Wirsing *et al.* 2008). Further examples include inter-tidal marine snails that adjusted their behaviour to brief high-risk periods but not lengthy low risk periods under predation threat from crabs (*Cancer producturs)* (Hamilton and Heithaus 2001), blackbirds (*Turdus merula*) that adjusted their behaviour in accordance with the risk associated with morning and evening peaks in human activity, and Siberian jays (*Perisoreus infaustus*) that avoided nest attendance at high risk times, compensating for these periods by increasing feeding effort at low risk times (Eggers *et al.* 2005).

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However, other studies on tadpoles (*Rana temporaria)* (Van Buskirk and Arioli 2002, Laurila *et al.* 2004), field voles (*Microtus agrestis*) (Koivisto and Pusenius 2003) and bank voles (*Clethrionomys glareolus*) (Sundell *et al.* 2004) have found no evidence to suggest that individuals fine-tune their behaviour temporally to risk, either because focal animals failed to assess differential risk (Van Buskirk and Arioli 2002) or failed to show a change in foraging effort in relation to changing proportions of risk (Laurila *et al.* 2004, Sundell *et al.* 2004). Other studies have showed mixed support: Psysid snails (*Physa gyrina*) held at continual risk showed an immediate increase in activity levels in response to an introduction of brief periods of safety into the test system, whilst snails held at continual safety showed moderate levels of activity throughout. However, snails only showed a weak reduction in activity when exposed to a pulse of danger (Sih and McCarthy 2002).

The most likely reason for the discrepancies amongst these studies is the element of artificiality in experimental designs. Some experiments, for example, found that animals soon became habituated to non-experimental cues (e.g. Koivisto and

Poisinius 2003, Laurila *et al.* 2004, Sundell *et al.* 2004), while other studies found that prey learned to respond to predators, but failed to learn the temporal variation in risk (Van Buskirk and Arioli 2002, Koivisto and Poisinius 2003, Sundell *et al.* 2004, Foam *et al.* 2005). The fundamental challenge to critically evaluating the risk allocation hypothesis is therefore to provide evidence of an adjustment in activity in response to a particular duration and intensity of predation risk.

Although anti-predator defences have been shown to have a strong genetic basis across a wide range of taxa (Huntingford and Wright 1993, Maloney and McClean 1995, Stoks *et al.* 2003), and many species show innate predator recognition (Monclus *et al.* 2005), most species require experience with predators and/or predator cues before recognizing and responding to predator risk (Tulley and Huntingford 1987, Hauser 1993, Chivers and Smith 1994, Burrows and Gibson 1995, Langen 1996, Chivers and Smith 1998, Griffin *et al.* 2000, 2001, Hanson and Cross 2001, Ferrari *et al.* 2006, Leduc *et al.* 2007, Berger and Gotthard 2008, Fraker 2008, Mathis *et al.* 2008, Vilhovenen *et al.* 2008).

Whereas experimental systems may often not allow enough time for prey individuals to learn about temporal variation in predation risk, the problem with observing natural patterns of non-naïve prey activity in response to pulses of risk is that one is looking at the finished product of such a learning process. Thus it is difficult to assess predation risk as the causative force which may have shaped such activity patterns. However, since predation risk is usually learned from a baseline of an initial risk-insensitive state in the development of most species (Hinde 1954, McLean and Rhodes 1991, Roth and Johnson 2004, Hayes *et al.* 2006, Hawkins *et al.* 2008, Hollen *et al.* 2008), the initial and eventual behaviour of juvenile prey animals may offer an opportunity to record such an adjustment.

Seal Island, South Africa provides an ideal study system for testing the risk allocation hypothesis because it is a natural predator-prey system with marked variation in the duration and intensity of predation risk. Sharks were not present during summer at Seal Island nor were they present at Egg Island on the west coast in either season. Thus, one can investigate seal behaviour at the same site with and without predators

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(Seal Island in winter and summer) and at islands with and without sharks (Seal Island and Egg Island, in both seasons). Together these factors offer an opportunity to gain insight into the relative contribution of temporal variation in predation risk to the behavioural patterns of seal in a natural system.

The aim of this study was thus to investigate the risk allocation hypothesis in a natural predator-prey system in which white sharks attack both adult (experienced) and juvenile (naïve) seals. I expected seal activity to be depressed within the danger zone during high risk periods compared to low risk periods. We predicted that patterns of temporal activity during the high risk winter season would differ significantly from the low risk summer season. Furthermore I predicted no difference in the pattern of temporal seal activity at the low risk Egg Island (safe site) in both seasons. Lastly, we investigate the ontogeny of juvenile (young of the year) behaviour following exposure to predation events, by comparing the temporal activity patterns of select juveniles at the beginning and end of the high predation season at Seal Island. We predicted that juveniles would learn to avoid the 'deep water habitat' (or danger zone) during high risk periods (i.e. immediately after sunrise) and conform to the temporal activity patterns of experienced adult seals.

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4.2. Methods

4.2.1. Study site

Data collection were performed at Seal Island, False Bay (where there are high levels of shark/seal interaction in winter) and at Egg Island, off Paternoster Rocks (where no seal/shark interactions have been documented). We collected data from early winter (June) to summer (December) at both sites. The relative predation risk between sites was determined by comparing the total number of attacks observed during ad-libitum observations on 15 field days at Seal Island in winter with 15 days in summer, and at Egg Island in winter and summer to test the generality of previous findings (Kock and Johnson 2006, Martin *et al.* 2005, Laroche *et al.* 2008) that winter predation risk is high relative to summer predation risk at Seal Island, and low at Egg Island relative to Seal Island. The study sites are described in detail in chapter two.

4.2.2. Telemetry

Seals were captured on each island using a modified hoop net (Gamel *et al.* 2005). Individuals were selected at random while attempting to minimize disturbance to the colony (i.e. we preferred animals that were resting behind rocks which facilitated a close approach and higher capture success). The front end of the hoop net comprised a PVC-cone that covered the eyes of a captured seals with just the mouth and nose protruding. This design allowed for the direct application of a gas mask without the threat of injury from bites. Both cows and juveniles were strapped to a restraining board whilst still in the hoop net. Isofluorine gas was then administered from a portable anaesthetic machine to adult females to facilitate their handling. Time of induction was 12.8±4.214 (Mean±s.dev.) minutes. Once anaesthetized, the cone was removed and seals were kept cool by frequent wetting of their flippers. Breathing rate was monitored throughout the capture and anaesthesia procedure.

Radio transmitters (120g, Advanced Telemetry Systems, Isanti, Minnesota) were deployed on six adult female seals and nine juveniles at Seal Island. Five adult female seals and six juveniles were fitted with radio transmitters at Egg Island. Radio transmitters ranged in frequency from 165 – 166 MHz at Seal Island, and between 148 and 149 MHZ at Egg Island. The transmitters were attached mid-

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dorsum, using quick setting epoxy glue (RV components, Johannesburg) as described in Gamel *et al.* (2005). Whilst waiting for the glue to set, seal length (in a straight line from the tip of the nose to the end of the tail), auxiliary girth (the width of the body immediately posterior to the pectoral flippers), and sex (by inspecting the ano-genital area (Huber 1994)) were recorded for each animal. Approximately five minutes before the seal was due to be released the volume of Isofluorine gas was reduced and oxygen flow was increased to minimize ataxia and thus improve recovery time. Mean time of capture to release was 34.875±14.466 (SD) minutes. Adult seals took 7.909±5.558 (SD) minutes to recover from anaesthesia.

Radio-instrumented animals were monitored with a receiver (Advanced Telemetry Systems, Isanti Minnesota) connected to an omni-directional antenna positioned at the highest available point in the middle of each Island. Each frequency was scanned for 60 sec every 15 min and presence/absence was recorded on a data collection computer (Advanced Telemetry Systems, Isanti, Minnesota) connected to the receiver. The data loggers and receivers were housed in a waterproof plastic container that was mounted at a height of approximately one metre from the ground on a metal pole. The data-logging receivers were powered by a 100Amp/hr Calcium battery that was kept in a positive state of charge by a solar-panel. Data was downloaded at frequent intervals, using a ribbon cable connected to a laptop computer and ATSWindRec_S® software (provided by Advanced Telemetry systems).

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The receiver could reliably detect transmitters at any place on the island and within the narrow shallow area around the island. The maximum distance that a hand held transmitter was detected from the Island was ca. 1000m and thus we assumed that no transmitter attached to a seal would be detected at a distance greater than this. Thus if a transmitter was not logged by the receiver then we assumed with reasonable confidence that the individual was not either on or in the vicinity ($\leq$ 1000m) of the island.

The presence of big rocks at both islands did result in the occasional ‘blind spot’ where the transmitter could not be detected by the receiver despite the seal being on the island. We attempted to reduce the probability of these false negatives by pooling four consecutive 15 min readings to provide a single result per hour. Thus all four readings would have to be absent for a transmitter to be recorded as being absent from the Island.

To control for noise resulting from receiver malfunction, we attached a reference transmitter to a rock approximately 100m away from the receiver, at both sites. If the reference transmitter was not recorded on the data logger, we removed the corresponding block of data from the analysis. This occurred only once, at the end of summer at Egg Island. As a result, we only used summer data prior to this (i.e. October and November, for both islands) in our analysis.

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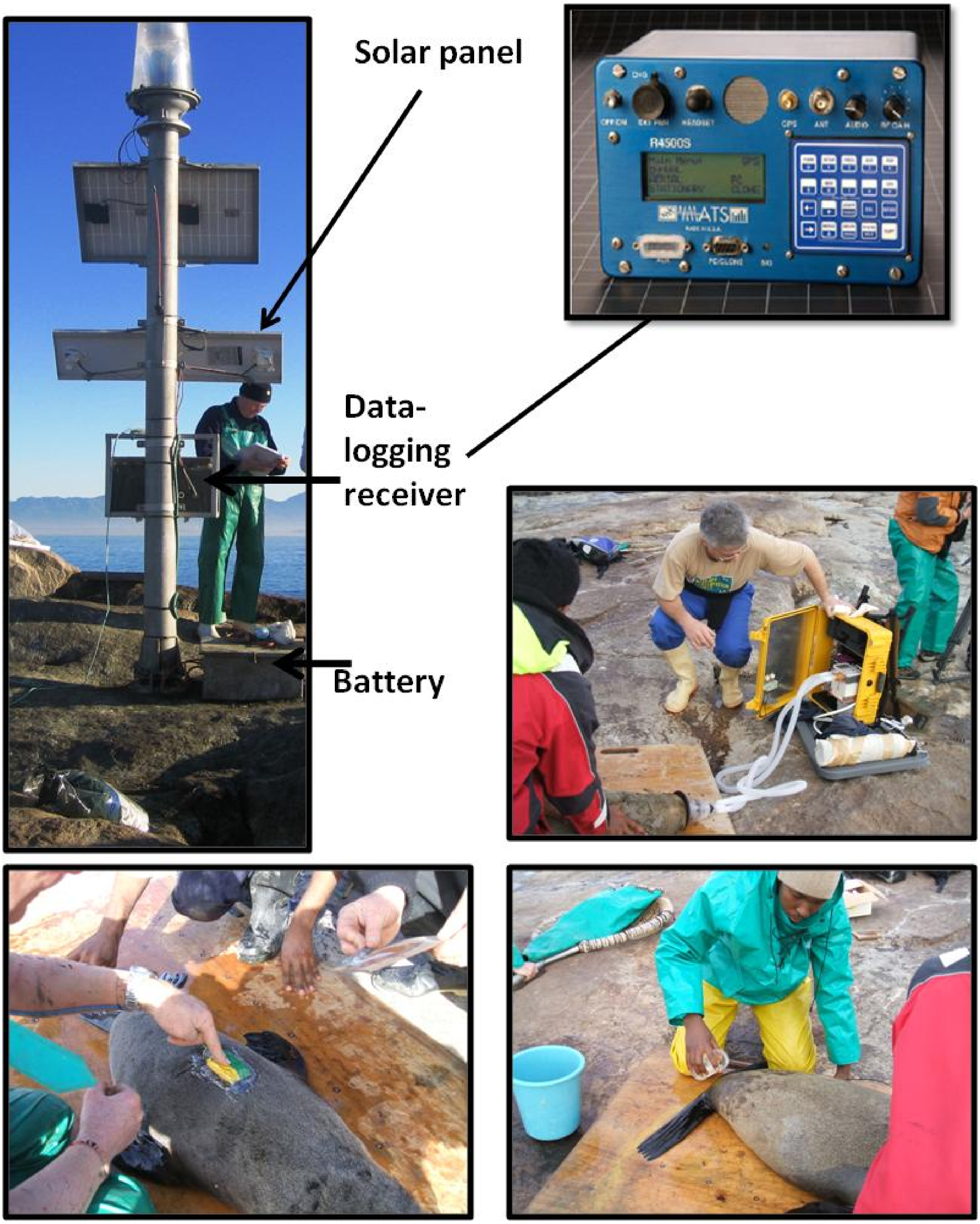

Figure 4.1. Telemetry set-up during this study (Seal Island shown). The data logging station was positioned at the highest point on the island, and consisted of a solar-powered data logger/receiver. This figure also illustrates the radio-tags that were attached to the seals.

4.2.3. Data analysis

Temporal patterns of presence/absence of both adult and juvenile seals were compared in three different ways:

1. Between different time periods at each island (using a Friedman's ANOVA for paired samples).
2. Between early winter and summer for adults at each island, and early winter and late winter for adults and juveniles (using a Wilcoxon matched paired t-test).
3. Between islands within each season (using a two-way factorial ANOVA).

Individuals were considered to have left the island if the receiver did not detect their transmitter for two hours after the first hour that the transmitter was not detected. The actual time of departure was then taken as the first hour that the animal was not detected at the island. The hour of returning was considered as the first hour that an individual was recorded to be back at the island following at least two absent hours. Arrival and departure times were grouped into eight time periods of equal duration. Time periods were not random, but designed to ensure that the peak predation time (i.e. 07h00– 09h59) fell within one time period.

To avoid pseudoreplication, the proportion of arrival and departure times in each of the time periods were calculated for each tagged individual, and statistical analysis carried out on the mean of these data. This resulted in relatively small sample sizes (n=6 for Egg Island and Seal Island adults, n=10 for Seal Island juveniles, and n=6 for Egg Island juveniles).

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4.3. Results

4.3.1. General results

The total number of attacks observed during ad-libitum observations at Seal Island in winter over 15 randomly selected field days was elevated (mean=8.375±6.177 s.d. attacks) relative to 15 randomly selected field days in summer (0 attacks) and at Egg Island (0 attacks in winter and summer).

There were no significant differences between adults (Mann-Whitney U, p>0.5 in all pair wise comparisons) or juveniles in mean (±S.D.) body length (136±14.112 cm, 91.467±3.806 cm), girth (102±3.536 cm, 66.533±1.836 cm) or body condition index (0.738±0.084, 0.729±0.037 cm) at Seal Island compared to that of adults (length= 139.2±6.656 cm, girth=102.92±3.536 cm, body condition index=0.751±0.058cm) and juveniles (length = 93.0± 6.292 cm, girth = 70.75±5.777 cm, body condition index= 0.761±0.059cm) at Egg Island.

There were no significant differences between the mean duration of time spent at Seal Island (97.458±63.908 hours) and Egg Island (101.526±44.448 hours). Seals at Seal Island did however, spend significantly more time away from the island (Mann-Whitney U, z=2.165, p=0.030, 249.5±88.236 hours) during any given trip compared to seals at Egg Island (65.105±35.519).

Seals spent a significantly greater proportion of their mean total time away from Seal Island (497.782±12.051 hours, 69.136%) compared to seals at Egg Island (334.509±14.68, 46.460%), and significantly less time at the colony (30.863% of total time at Seal Island=222.218±11.75 hours; 53.540% of total time= 385.490±10.714 hours).

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4.3.2. Temporal adjustments by adult seals

Hourly differences in seal movement

In winter, adult seals left Seal Island significantly more often (Friedman's ANOVA, F=17.429, df=7, n=5) between 04h00 and 06h59 (before sunrise) than during any time category between 07h00 to 19h59; and also between 20h00 to 22h59 and between 07h00 and 10h59 (Wilcoxon paired t-tests, p<0.05, table 4.1., figure 4.1.). Seals were observed returning to the island significantly more often between 20h00 and 03h59 (Friedman's ANOVA, F=15.37, df=7, n=5) than between 07h00 and 10h59 (high risk), and 14h00 and 16h59 (Wilcoxon paired t-tests, p<0.05).

At Seal Island, seals did not leave or return significantly more or less during any time category during summer. Similarly, at Egg Island seals did not leave or return significantly more during any particular time period compared to any other.

Seasonal comparison

Seals were less likely to leave or return to Seal Island between 07h00 and 09h59; and 10h00 and 12h59 during winter than during summer (Wilcoxon paired t-test, z=0.043, p<0.05 for all four tests, figure 4.2., table 4.2.). Seals at Seal Island were significantly more likely to leave and return between 04h00 and 06h59 in winter than in summer (z=0.043, p<0.05 in both cases), and left significantly more between 17h00 and 19h59 (z=2.022, p=0.047) in winter than they did in summer. Again, seals showed no significant temporal discretion at Egg Island during winter or summer.

Interactions between site and season

There was a significant interaction between site and season in all of the time-periods between 04h00 and 06h59 for both leaving and returning seals; and for leaving seals between 17h00 and 19h59 (p<0.05, see table 4.3), with no significant confounding effects of site and season for the time periods between 07h00 and 10h59am.

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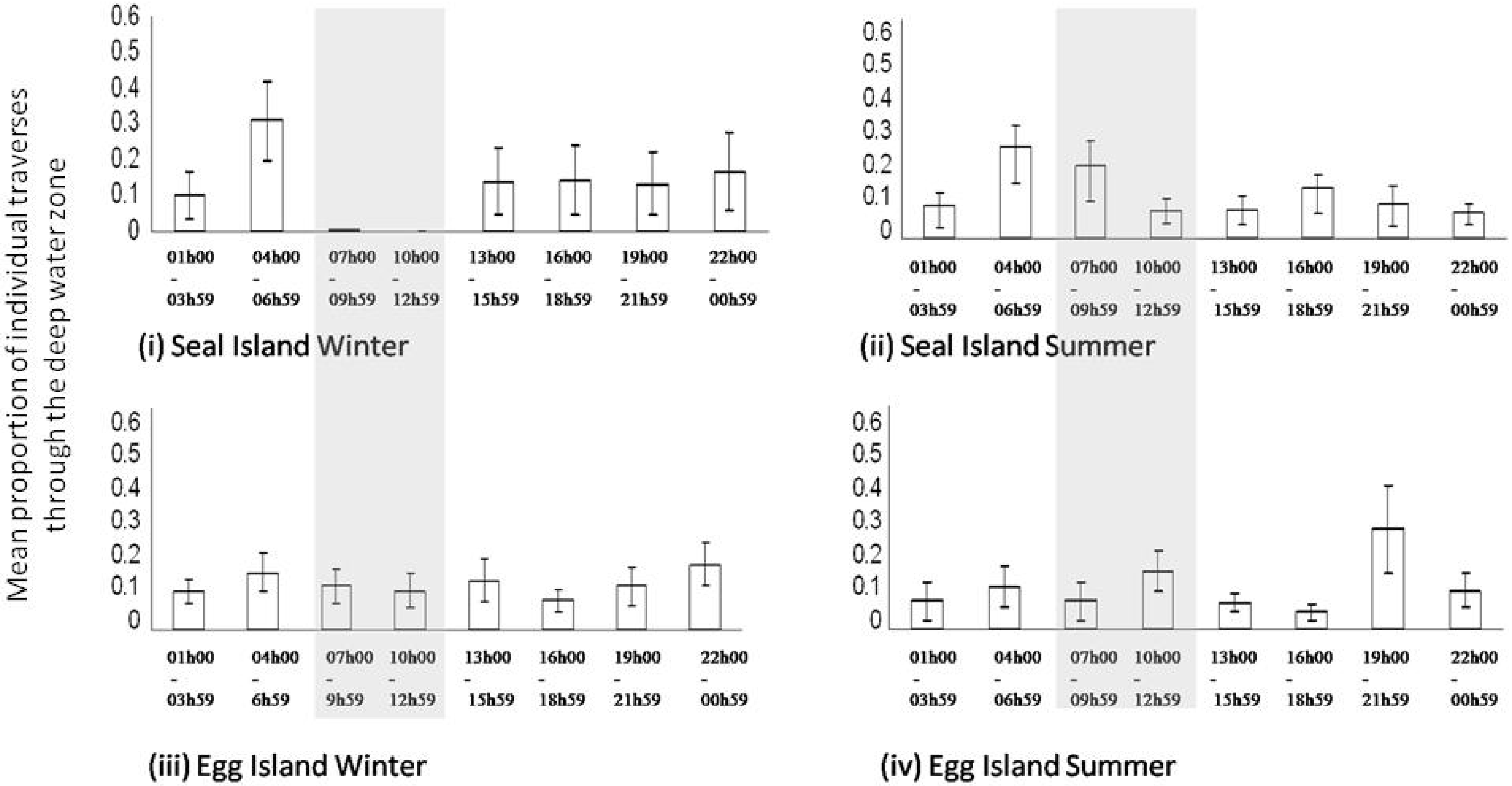

(i) Seal Island Winter

(ii) Seal Island Summer

(iii) Egg Island Winter

(iv) Egg Island Summer

Figure 4.2. Mean proportion of radio-tagged seals that left or arrived at either Seal (i and ii) or Egg Island (iii and iv) within three hour intervals in both winter (i and iii) and summer (ii and iv). The shaded time zone represents the period of highest predation at Seal Island in winter.

Table 4.1. Friedman's ANOVA of the mean proportion of seals arrived or left either Seal or Egg Island at different time periods in both winter and summer. Time periods for which the proportion of seals either leaving or returning was significantly different from other time periods are indicated in the last two columns (higher and lower activity respectively).

Direction	**Site**	**Season**	**Friedman's ANOVA (n=7)**	**n**	**p - value**	**Higher Activity**	**Lower Activity**
Leaving	Seal Island	Winter	17.429	5	**0.015**	04h00- 06h00 07h00 - 21h59	All other periods
		Summer	10.872	5	0.120		
	Egg Island	Winter	5.325	5	0.620		
		Summer	8.986	5	0.253		
Returning	Seal Island	Winter	15.370	5	**0.032**	All other periods 19h00-03h59	All other periods 07h00-12h59
		Summer	3.117	5	0.874		
	Egg Island	Winter	7.570	5	0.370		
		Summer	6.977	5	0.431		

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Table 4.2. Matched pair’s comparison of the mean proportion of seals leaving and returning to both Seal and Egg Islands in winter and summer. The table shows time periods in which the proportion of individual seal movement varied significantly between seasons.

	Time	**Site**	**z-stat**	**n**	**p-value**	**Direction (season with highest activity)**
Leaving	04h00-06h59	Seal Island	2.023	5	0.043	winter
	07h00-09h59	Seal Island	2.023	5	0.043	summer
	10h00-12h59	Seal Island	2.023	5	0.043	summer
	19h00-21h59	Seal Island	2.023	5	0.043	summer
Returning	04h00-06h59	Seal Island	2.023	5	0.043	winter
	07h00-09h59	Seal Island	2.023	5	0.043	summer
	10h00-12h59	Seal Island	2.023	5	0.043	summer

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Table 4.3. Two-way factorial ANOVA indicating time periods for which there was a significant interaction between site and season.

There were no significant effects of either site or season within each of indicated time bins.

	Time	Significant effects	F-value	p-value
Leaving	07h00-09h59	Intercept	21.316	0.000
		Site*season	8.895	0.007
Returning	07h00-09h59	Intercept	12.056	0.004
		Site*season	4.755	0.047
	10h00-12h59	Intercept	14.653	0.002
		Site*season	4.755	0.047

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Shifts in arrival and departure times for adult and juvenile seals in early versus late winter at Seal Island

Adult seals were not significantly more or less likely to leave or return to the island during different time periods in either summer or winter at Egg Island (figure 4.2., table 4.4.). Adults seals left Seal Island significantly less often (Wilcoxon paired tests, z=1.997, 2.022, p<0.05) between all time categories falling between 07h00 and 18h59 than between 04h00 to 06h59 during early winter (table 4), and between 07h00 and 12h59 than between 19h00 and 21h59 during late winter. Seals returned to the island significantly more often (Wilcoxon paired t-tests, z=1.990, p<0.05) between 22h00 and 03h59 than during the time periods between 07h00 and 09h59, and also between 16h00 and 18h59 during both early and late winter. Juvenile seals showed no temporal discretion when either leaving or returning to Seal Island in early winter (table 4.4), but juveniles in late winter were significantly (Wilcoxon paired tests, z=1.991, 2.010, 2.240 p<0.05) less likely to leave and return during all periods between 07h00 and 15h59 than between periods 19h00 and 21h59 (leaving) and 22h00 and 03h59 (returning). At Egg Island, in both early and late winter leaving and returning juvenile seals left and returned significantly more often between 01h00 and 06h59 than between periods between 10h00 and 18h59 (Wilcoxon paired tests, z=1.990, 2.023, p<0.5).

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Seasonal comparisons of leaving and returning activity during different time categories

The times during which juveniles left and returned to and from Seal Island varied significantly across seasons at Seal Island, but not at Egg Island. Juveniles at Seal Island left the island more frequently between 07h00 and 12h59 in late winter compared to early winter (Wilcox paired t-tests=2.023, 2.201, 2.521, p<0.05), and more frequently between 04h00 and 06h59 and 19h00 to 21h59 in late winter compared to early winter (Wilcox paired t-tests, z=2.023, p=0.043).

Returning juveniles left the island significantly (z=1.992, p=0.046, n=9) more often between 01h00 and 03h59 during late winter than during early winter, and significantly less often (z=2.023, 2.197, p<0.043, n=9) between 07h00 and 18h59.

Juveniles at Egg Island also returned less often between 16h00 and 18h59 in late winter compared to early winter (z=2.201, p=028), and left more often between 01h00 and 03h59 (z=2.201, p=0.028). Seals showed significant seasonal variation in times that they left and returned to Egg Island (Wilcox paired t-tests, p>0.05). Adult seals at Seal Island left and returned more between 10h00 to 12h59 in late winter compared to early winter (Wilcox paired t-tests, z=2.023, p=0.043), but otherwise showed no other seasonal variation in leaving and returning times.

*Site*season interactions*

A two-way factorial ANOVA on leaving and returning times showed significant effects of the interaction between site and season in all of the periods between 04h00 and 12h59 for leaving seals and in all periods between 01h00 and 12h59 for returning seals. In leaving seals, the period between 07h00 and 09h59 was confounded by a significant effect of site (F=5.587, p=0.023), and in returning seals the period between 10h00 and 12h59 was confounded by age (F=2.948, p=0.033).

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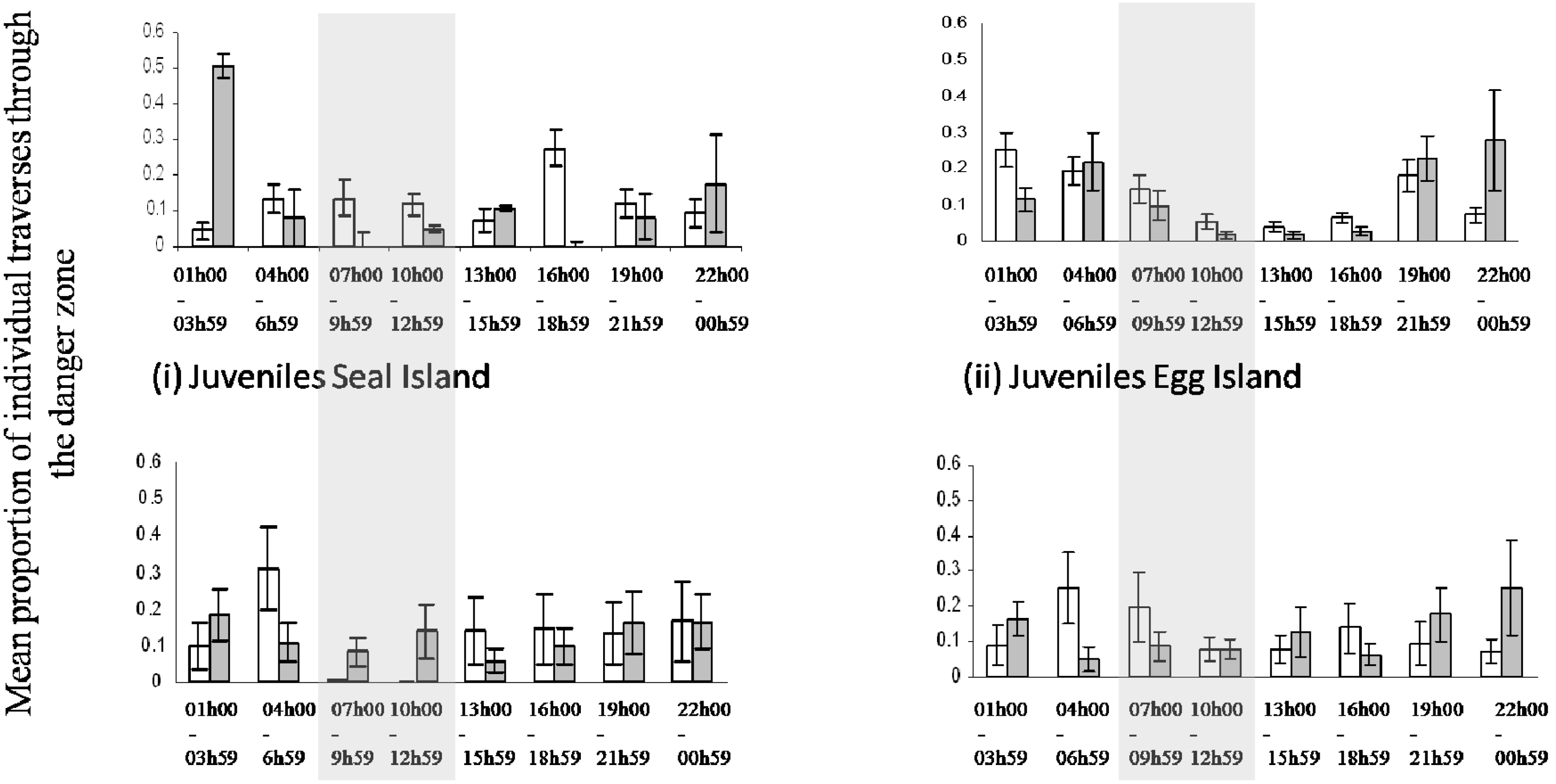

(i) Juveniles Seal Island

(ii) Juveniles Egg Island

(iii) Adults Seal Island

(iv) Adults Egg Island

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Figure 4.3. Mean proportion of ratio-tagged adult (iii and iv) and juvenile (i and ii) seals that left or arrived at either Seal (i and iii) or Egg Island (ii and iv) within three hour intervals in both winter (i and iii) and summer (ii and iv). The shaded time zone represents the period of highest predation at Seal Island in winter.

Table 4.1. Friedman's ANOVA of the mean proportion of radio-tagged adult and juvenile seals that arrived or left either Seal or Egg Island's in different time periods during early and late winter. Time periods for which the proportion of seal movement was significantly different from other time periods are shown.

Direction	Age class	Site	Season	Friedman's ANOVA (df=7)	n	p – value	Higher activity	Lower activity	Z-stat	p-value
Leaving	Adults	Seal Island	Early winter	17.429	5	0.015	04h00–06h59	07h00-18h59	2.022	0.042
							19h00-00h59	07h00-12h59	1.991	0.046
			Late winter	15.941	5	0.026	All other	07h00-09h59	2.020	0.043
		Egg Island	Early winter	5.325	5	0.620				
			Late winter	5.187	5	0.637				
	Juveniles	Seal Island	Early winter	9.974	9	0.190			2.022	0.043
			Late winter	20.510	9	0.005	19h00-21h59	07h00-18h59	2.240	0.025
		Egg Island	Early winter	15.074	6	0.035	19h00-06h59	07h00-09h59	1.991	0.047
			Late winter	19.246	6	0.008	19h00-06h59	13h00-18h59	2.010	0.046
Returning	Adults	Seal Island	Early winter	15.370	5	0.032	22h00-03h59	07h00-12h59	1.991	0.047
							16h00-18h59			
			Late winter	9.973	5	0.190				
		Egg Island	Early winter	7.570	5	0.370				
			Late winter	4.513	5	0.719				
	Juveniles	Seal Island	Early winter	9.974	9	0.190				
			Late winter	15.370	9	0.032	22h00-03h59	07h00-12h59;	1.990	0.043
							16h00-18h59			
		Egg Island	Early winter	20.725	6	0.004	01h00-06h59	10h00 -21h59	1.990	0.047
			Late winter	15.074	6	0.035	22h00 – 06h59	10h00-21h59	0.022	0.005

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4.4. Discussion

The risk allocation hypothesis predicts that animals will optimally allocate activity across different states of risk (Lima and Bednekoff 1999). Animals experiencing short periods of high risk and long periods of comparative safety are predicted to adjust their activity to reflect this differential temporal risk.

At Seal Island, both leaving and returning adult seals avoided arriving and returning to the island (i.e. traversing the “danger zone”) for the duration of the high risk period, in contrast to adult seals at Egg Island that showed no comparative avoidance of this time period. Seals at Seal Island left and returned to the island mostly at night. Studies on shark movement have suggested that sharks move away from the island at night (A. Kock *pers. comm*.) and thus the increased movement of seals between dusk and dawn would suggest an anti-predatory tactic. However, this pattern of increased movement to and from the island at night is also evident at the comparatively predator free Egg Island and furthermore, in summer at Seal Island when sharks are scarce. Thus the temporal peak in nocturnal activity to and from both islands most probably relates to temporal patterns of food availability versus predator avoidance behaviour. Cape fur seals feed predominantly on prey items that perform diel migrations in the water column (De Bruyn *et al.* 2003, 2005) and that are more abundant close to the surface of the ocean at night than during than day. Thus there are substantial energetic advantages to foraging at night when preferred prey items such as hake and squid (Arnould and Hindell 2001, Gamel *et al.* 2005) are closer to the ocean surface.

The potentially confounding effect of foraging on the temporal patterns of movement to and from the island highlights the importance of being able to compare movement with high and low predation risk at the same island. Adult seals avoided leaving or returning to Seal Island during the brief, high predation risk period, corroborating the findings of Laroche *et al.* (2008). However, a negative correlation between the level of seal activity within the ‘danger zone’ and predation risk is not sufficiently robust as evidence in support of the risk allocation hypothesis. Rather one needs to demonstrate that individuals adjust their movement patterns in response to differing levels of risk.

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In this study we provide evidence for risk adjustment in both experienced adult and naïve juvenile seals. Experienced adult seals reduced their frequency of arrival and departure at Seal Island during the high risk time of day (sunrise to 09h59) in winter when sharks were abundant but not during summer when predation risk was low. This temporal adjustment between seasons was not evident at Egg Island (the low risk site), with adult seals showing no discrimination in their use of this time period in either season. A temporal shift in arrival and departure times during the high risk period was also evident in the predator-naïve juveniles at Seal Island, but not at the low risk Egg Island. At the start of winter, when the sharks first arrive at the island (Martin *et al.* 2005) juveniles exhibited no avoidance of the high risk period. However by the end of winter, the same juveniles exhibited a similar pattern to the adults and avoided movement on or off the island during the high risk period after sunrise.

It would thus appear that adults adjust their temporal movement patterns in accordance with both daily and seasonal variation in predation risk at Seal Island while juveniles learn to avoid the times of day when predation risk is highest. Prey animals usually learn about predators either by encountering them directly or by being in close proximity to a conspecific that encounters a predator (e.g., Diaz-Uriarte 1999, Griffin and Evans 2003, Cook and Mineka 1990). Alternatively prey can learn to avoid predators by acquiring information on them through social learning (Johnsson and Sundström 2006, Brydges *et al.* 2008, Mazur and Seher 2008) which entails naïve individuals acquiring information from predator experienced individuals by observing their reaction to a non-lethal cue (Ekloev and Person 1996, Chivers and Smith 1998, Chapman *et al.* 2007, Mirza and Chivers 2002, Gil-da-Costa *et al.* 2003, Arágon *et al.* 2006, Vilhunen *et al.* 2005, Shier and Owings 2006, Leduc *et al.* 2007, Laakkonen and Hirvonen 2007, Ferrari and Chivers 2008, Mathis *et al.* 2008). Social learning features strongly in systems with pronounced parental care (Tulley and Huntingford 1987), and some investigators suggest that adult/juvenile interactions may constitute a proximate mechanism by which juveniles can develop anti-predator defences prior to direct experience with a predator (Goodey and Liley 1986; Tulley and Huntingford 1987).

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How individuals learn about predation risk may have important implications for the validity of the risk allocation hypothesis within a given system. We postulate that if animals are not capable of learning about predation risk then it is difficult to envisage, at a proximate level, how they could adjust their temporal activity patterns in response to predation risk. When predation pressure is extremely high and spatio-temporally predictable, such as at Seal Island, then the learning and subsequent adjustment of temporal activity, in response to predation risk may be feasible. Furthermore, if there are strong cues associated with predation (e.g. breaching) then prey individuals may be able to acquire information about predation risk sufficiently fast to make behavioural adjustments to reduce predation risk.

Together the results presented in this paper have important implications for the risk allocation hypothesis. Firstly, we provide evidence in support of the prediction that animals adjust their activity in relation to brief, high risk periods within a natural system. The robustness of this result is strengthened by the absence of any temporal adjustments in activity patterns to and from Egg Island, an island with low predation risk. Secondly, these results were obtained from a predator-prey system in which there is ample opportunity for individuals (both experienced and naïve in this system) to learn about differential predation risk and therefore adjust their temporal activity patterns with time. The mechanism(s) and cue(s) for learning about differential temporal risk remain to be elucidated within the current system.

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Chapter 5

The selfish herd

Sharks shape the geometry of a selfish seal herd: experimental evidence on decoys

A paper based on the results presented in this chapter was published as:

Alta De Vos and M. Justin O'Riain
Sharks shape the geometry of a selfish seal herd: experimental evidence from seal decoys
Biol Lett 2009 : rsbl.2009.0628v1-rsbl20090628.

Abstract

Many animals respond to predation risk by forming groups. Evolutionary explanations for group formation in previously ungrouped, but loosely associated prey have typically evoked the selfish herd hypothesis. However, despite over 600 studies across a diverse array of taxa, the critical assumptions of this hypothesis have remained collectively untested, owing to several confounding problems in real predator–prey systems. To solve this, we manipulated the domains of danger of Cape fur seal (*Arctocephalus pusillus pusillus*) decoys to provide evidence that a selfish reduction in a seals' domain of danger results in a proportional reduction in its predation risk from ambush shark attacks. This behaviour confers a survival advantage to individual seals within a group and explains the evolution of selfish herds in a prey species. These findings empirically elevate Hamilton's selfish herd hypothesis to more than a 'theoretical curiosity'.

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5.1. Introduction

Predation is one of the main evolutionary forces driving the formation of groups which provide individuals with various benefits related to detecting, confusing, deterring and mobbing predators (reviews in Krause and Ruxton 2002, Cresswell 2008, Caro 2005). At the simplest level, when a predator can only target one or a few members of a group at a given time (Foster and Terherne 1981), an individual may be afforded a dilution of risk. Risk is often assumed to be equally shared by members of a group, but differential risk is a real attribute for individuals within a group and may be the very driver of how they behave within groups. William Hamilton's (1971) selfish herd hypothesis has arguably been the most popular model used to explain how differential risk may cause loosely associated prey individuals to form compact groups (Hamilton 1971, Vine 1971, Morton *et al.* 1994, James *et al.* 2004).

In Hamilton's simplest model, loosely associated surface-living individuals are preyed upon upon by a below-surface dwelling predator. The predator randomly appears at the surface and attacks the nearest prey individual from the point at which it emerges. Surface-living individuals thus have "domains of danger" - the space around an individual within which it will be the "closest" individual should the predator appear within that space. The larger this area, the greater the individual's predation risk relative to that of its neighbours. By moving towards neighbours an individual can reduce the size of its "domain of danger", which, hypothetically, translates into lower predation risk (Hamilton 1971). Hamilton argued that if all individuals move in this way, compact groups may result.

The elegance of the selfish herd hypothesis (SHH) has endeared it as a framework within which to interpret the behaviour of prey in response to predators in a diverse array of taxa including fish (Caro 2005, Krause and Ruxton 2002, Krause 1994), mammals (Krause and Ruxton 2002, Krause 1994, Fitzgibbon 1990), birds (Quinn and Creswell 2006, Krause and Ruxton 2002, Krause 1994, Watt and Mock 1987), amphibians (Watt *et al.* 1997), spiders (Uetz 1993), insects (Romey and Wallace 2007, Millinski 1977) and crustaceans (Viscido and Wethey 2002). Despite its popularity, the critical assumptions of the hypothesis have remained collectively

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untested, owing to several confounding problems in real predator-prey systems (e.g. Romey and Wallace 2007, Quinn and Creswell 2006, Uetz 1993, Fitzgibbon 1990, Pulliam 1973).

The major body of evidence in support of the selfish herd hypothesis emanates from studies that have: 1) successfully quantified increased cohesiveness of groups when exposed to predators (Viscido 2003, Watt *et al.* 1997), 2) shown that individuals prefer central to peripheral positions within a group (Caro 2005, Krause and Ruxton 2002, Krause 1994, Watt and Mock 1987), and 3) that individuals in the centre of a group have less risk relative to peripheral individuals (Uetz 1993, Milinski 1977, see table 1). However, the results of these studies are not unequivocal. The classification of centre versus edge individuals is open to bias (Stankowich 2003, Viscido 2003), there is ambiguity in the literature as to where animals are more at risk (Caro 2005, Krause and Ruxton 2002, Watt *et al.* 1997, Krause 1994) and results at group centres and edges may be strongly confounded by other benefits and costs of grouping (Caro 2005, Krause 1994, Fitzgibbon 1990). Furthermore, the central prediction that an individuals spacing affords it differential predation risk has been largely neglected with, to the best of my knowledge, only one study having shown that predators (sparrow hawks) target more widely spaced prey (redshank), relative to non-attacked neighbours whilst controlling for predator confusion, centre/edge positioning and, to some extent, vigilance (Quinn and Cresswell 2006).

Indeed, the presence of confounding differential agents of risk within groups may be the most pertinent complication to SHH herd investigations. Predators often avoid selecting more vigilant individuals (Quinn and Creswell 2006), might find grouping individuals more difficult to target (Caro 2005, Krause and Ruxton 2002), might preferentially target prey individuals of different body size (Romey and Wallace 2007, Uetz 1993), experience (Romey and Wallace 2007, Uetz 1993, Milinski 1977), and/or state of hunger (Romey and Wallace 2007, Milinski 1977).

The original SHH was primarily a model for the evolution of gregarious behaviour in response to predation pressure (Hamilton 1971). As such the major predictions that need to be satisfied for its proof are difficult to test in real world systems which are themselves a product of the selection pressures that one is interested in measuring.

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Consequently, evidence on cohesiveness, competition for within-group positions, or edge/centre safety cannot falsify the SHH. Groups may have been maintained by other strategies, such as the pure dilution effect (Milinski 1977), vigilance (Pulliam 1973), or predator confusion (Krause and Ruxton 2002, Caro 2005). Conversely, the disadvantages of grouping (Krause and Ruxton 2002, Caro 2005) might subsequently have countermanded selfish herds.

The critical corroboration of the SHH has to come from demonstrating that it's central concept – the domain of danger – is a biological reality (i.e. the size of the domain of danger is proportional to predation risk) and that it alone embodies differential survival probability and is subject to selection pressure. This study which is based on the interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) provides an opportunity to test this central concept.

There are a number of reasons why both the dynamics of the predator-prey relationship in addition to spatial and temporal variation in predation risk at Seal and Egg Islands provide an excellent system for testing the SHH. Firstly, there are large numbers of loosely aggregated seals at both islands but only predators at the former. Thus it is possible to investigate whether loosely associated seals which are effectively overdispersing on clumped resources (viz. commuting from a breeding island to preferred feeding areas) are driven to form compact groups under conditions of differential risk. Secondly, there is a distinct spatial separation of foraging and predation zones (Rand 1969, Laroche *et al.* 2008). Seals must traverse the "danger zone" adjacent to the island, and groups that form prior to departure from the island subsequently break up, once out of the danger zone (Rand 1969, Laroche *et al.* 2008). Furthermore, predator-prey activity is spatiotemporally confined and predictable (Laroche *et al.* 2008), and the system, where the predator appears by surprise within a group is one that strongly resembles Hamilton's original hypothetical model. Most propitiously, sharks identify their prey using surface moving silhouettes (Laroche *et al.* 2008), which allows for an opportunity to manipulate the system by constructing artificial seal groups (and thus silhouettes) with variable domains of danger for the group members.

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The use of decoys offers a unique and unusual opportunity to test ideas on how predators target their prey. Not only can exact distances between “individuals” be measured (and risk probability assigned to specific domains of danger), but seal size, group size and group composition can all be manipulated to test specific predictions of the selfish herd hypothesis. Furthermore, and uniquely amongst predator-prey systems, it offers a test of the selfish herd hypothesis that controls for vigilance, the confusion effect and phenotypical and behavioural variability within groups.

In this chapter, I test the major predictions of the selfish herd hypothesis in a system where the major assumptions of Hamilton’s (1971) model hold true. I test whether loosely aggregated seals form compact groups when exposed to high predation risk and whether grouping reduces the relative predation risk of individuals. Furthermore, I investigate the central prediction of the selfish herd hypothesis, namely, that the size of a seals domain of danger within a group is proportional to its predation risk.

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Table 5.1. A summary of select publications including the authors, their study animals, the prediction(s) tested and the main finding of the research relevant to the testing of Hamilton's (1971) selfish herd hypothesis.

Author(s)	**Year**	**Prey**	**Predator**	**Prediction**	**Result**
Andersson and Wiklund	1978	Fieldfare	Crow, woodpecker, jay, squirrel, mustelid	Gradients of risk within groups	Predation risk higher at periphery.
Beachamp and Ruxton	2008	Semi-palmated sandpipers	Raptor	Gradients of risk within groups	Semi-palmated sandpipers on the riskier side of flocks were more vigilant and pecked at a lower rate than those in the centre of the flocks and those on the less risky side.
Becker	1995	Common tern	Herring gull	Gradients of risk within groups	Predation risk higher at periphery
Blanchard *et al.*	2008	Impala	Carnivores	Spatial preference; gradient of risk within groups	Peripheral individuals more vigilant than centre ones
Brunton	1997	Least tern	Black-crowned night heron, crow	Gradients of risk within groups	Predation risk higher in the centre of the group
Brunton	1997	Least terns	Night herons and crows	Gradients of risk within groups	Most heron predation occurred in centre of the colony, highest crow predation occurred at the edge of the colony
Buckley and Buckley	1977	Royal tern	Laughing gull	Gradients of risk within groups	Predation risk higher at periphery
Brown and Brown	1987	Cliff swallow	Bull snake, rattle snake	Gradients of risk within groups	Predation risk higher at periphery
Carere *et al.*	2008	Starling	Peregrine falcon	Increased cohesiveness	Significantly higher frequencies of compact and large flocks were observed in the roost with high predation pressure, while small flocks and singletons were more frequent at the roost with low predation pressure.

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Author(s)	**Year**	**Prey**	**Predator**	**Prediction**	**Result**
Hoogland	1981	Prairie dogs	Not mentioned	Spatial preference	Centre individuals were less alert, and central positions preferred.
Horn	1968	Brewer's blackbird	Mainly mammals, snakes	Gradients of risk within groups	No difference in risk between centre and edges of groups.
Patterson	1965	Black-headed gull	Fox, hedgehog, crow, gulls	Gradients of risk within groups	Predation risk higher at periphery.
Krause	1993	Dace and minnows	Schreckstoff (chemical)	Spatial preference	When frightened minnow moved into the centre of the group.
Kruuk	1964	Black-headed gull	Fox, hedgehog, crow, gull	Gradients of risk within groups	Predation risk higher at periphery.
McLain *et al.*	2005	Fiddler crabs	Avian	Increased cohesiveness	Crabs at higher risk were more likely to form small, compact mini-herds.
Millinski	1977	Water fleas	Stickleback	Gradients of risk within groups	Preferentially attack stragglers compared to group members and edge more than the centre. Densest spots were preyed upon more.
Orpwood *et al.*	2008	Minnows	*Esox lucius*	Increased cohesiveness	Minnows increased compaction and formed shoals in the presence of *Esox lucius*. Result only noted in simply structured habitat, with no other cover.
Parrish	1989	Adelie Penguin	Piscean	Gradients of risk within groups	83% of risk was encountered by centre individuals.
Picman *et al.*	2002	Yellow-headed blackbird	Not mentioned	Gradients of risk within groups	47% of experimental nests in the middle of a colony were depreyed upon compared with 65% on the periphery.
Radford and Ridley	2007	Pied babblers	Avian	Gradients of risk within groups	Foraging pied babblers were less vigilant when in larger groups, in the centre of a group and in closer proximity to another group member.
Rayon and Uetz	1993	Spider	Wasp	Gradients of risk within	62% of attacks occurred on edge.

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groups

Author(s)	**Year**	**Prey**	**Predator**	**Prediction**	**Result**
Schaller	1964	White pelican	Mammalian	Gradients of risk within groups	Predation risk higher at periphery.
Seppala *et al.*	2008	Fish groups	Avian	Increased cohesiveness	Increased cohesiveness of fish groups in relation to predation by avian predators.
Siegel-Causey and Hunt	1981	Double-crested and Pelagic cormorant	North-western crow, glaucous-winged gull	Gradients of risk within groups	Predation risk higher at periphery.
Simpson *et al.*	1987	Great blue heron	Raven, bald eagle, raccoon	Gradients of risk within groups	Predation risk higher at periphery.
Speakman *et al.*	1995	Pipistrelle bats	Not mentioned	Increased cohesiveness	Extent of clumping greater during the first half of bat emergence from caves, when light levels and predation risk high.
Spieler and Linsenmair	1999	Tadpoles of the common toad	Carnivorous tadpole	Increased cohesiveness	Increase in group cohesion.
Strassman	1991	Wasps	Not mentioned	Gradients of risk within groups	No difference in the success of central or peripheral nests.
Taylor	1976	Adelie Penguin	Antactic skua, brown skua, kelp gull, giant petrel	Gradients of risk within groups	Predation risk higher at periphery.
Treves *et al.*	2001	Howler monkeys	Not mentioned	Spatial preference	Scanned more when there were no neighbours within 2m of focal monkey, compared to when there were two neighbours.
Uetz *et al.*	2002	Mexican colonial web-building spider	Wasp	Gradients of risk within groups	Centre individuals at lower risk than edge individuals, received early warning about predation risk though vibrations in the colony web.
Van Vessem and	1986	Gray heron	Corvids	Gradients of risk within	No difference

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Draulans				groups	
Author(s)	**Year**	**Prey**	**Predator**	**Prediction**	**Result**
Watt and Mock	1987	Grey-breasted martins	Not mentioned	Spatial preference, increased Cohesiveness	Central roosting positions were contested more fiercely (78 - 83% of the time), and were less likely to be abandoned voluntarily.
Watt *et al.*	1997	Tadpoles of the common toad	Predator odour	Increased cohesiveness	Tadpole groups became more cohesive when they smelled a predator.
Wcislo	1984	Digger wasp	Parasites	Gradients of risk within groups	Nearest-neighbour distance in parasites nests greater than that of the population as a whole and a roughly linear increase in parasitism as nearest neighbour distance increased.
Wiklund	1982	Fieldfare	Crow, woodpecker, jay, squirrel, mustelid	Gradients of risk within groups	Predation risk higher at periphery.
Wiklund and Andersson	1994	Fieldfare	Crow, woodpecker, jay, squirrel, mustelid	Gradients of risk within groups	Predation risk higher at periphery.

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5.2. Methods

5.2.1. Study sites

I collected data for this chapter at Seal Island, False Bay where there are high levels of shark predation during winter. I divided the deep water zone into a “danger zone” within 1.5km of the island in which shark attacks were common and a “safe zone” more than 1.5km away from the island in which attacks were rare. Both study sites are described in detail in chapter two.

5.2.2 The spatial geometry of seal groups

To answer questions on the spatial geometry of real seal herds, we followed seal groups with a helicopter and recorded the movement patterns, spatial geometry and size of individual seals within seven groups (a total of 60 individuals, in groups ranging in size from 3 – 17, followed on two different days) with a digital video camera. Seal groups were filmed leaving from the South-western side of the island for a total distance of approximately two kilometres. The duration and route travelled by the group was recorded with a handheld GPS (Garmin E-trex) within the helicopter. Southwell (2005) found that a helicopter flying directly over and lower than 130m altitude had no effect on the behaviour of three species of Pinnipeds and two species of Penguins. A similar result was obtained for this study and the seals appeared to be unaware of the helicopter unless the shadow of the aircraft passed directly over them. Shadows elicited classical anti-predator behaviour (rapid evasive manoeuvers) and these events were thus excluded from the subsequent analyses on group geometry and behaviour. For the most part we simply requested that the pilot avoids casting a shadow on the group to reduce any observer effects.

Video footage taken from aerial follows was subsequently analyzed using video software (Moviemaker) to freeze-frame groups and estimate distances between seals. There was a similar (normal) distribution of body sizes within all seven groups, and no significant difference in the mean body size of individuals between groups. Adult female seals are on average 136±14.112cm in length and this mean was used as the metric upon which other measurements within the group (e.g. distances between individuals) were estimated. Although this approach could not be

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regarded as accurate from an absolute perspective it is important to bear in mind that comparisons were relative as they were between the same individuals in the same groups under two conditions of predation risk (high versus low). I calculated group compaction by averaging the domains of dangers, described in more detail below, for all individuals within a group and compared these values inside versus outside the danger zone using a paired t-test, after testing for normality and homogeneity of variances.

5.2.3 Decoy experiments

I used styrofoam® boards with black ventral surfaces, to construct identical seal decoys which were then fixed into positions on a raft, using lightweight reed poles secured to the dorsal surface of each decoy. By varying the distances between each decoy within a group, I could produce variable and repeatable domains of danger. The use of standardised decoys also allowed me to control for all within-group phenotypic attributes. Furthermore, because decoys cannot react to predators I was able to control for prey/group effects, including vigilance and predator confusion. Decoy rafts, comprising two different arrangements of four and five decoys respectively, were towed at a distance of 30m behind a 5m semi-rigid boat at an approximate speed of 7km.h-1. Both seals and sharks were habituated to the close proximity of motor boats as both tour operators and researchers have used boats to observe shark/seal interactions at the island for more than ten years. I towed the decoy raft through five 1km long transects on 16 separate days and recorded a total of 36 independent shark attacks. After each predation event I recorded which decoy had been attacked. Decoys were designed to break free from the raft upon attack, reducing the chances of injury to the shark and enabling a conclusive assessment of the targeted decoy.

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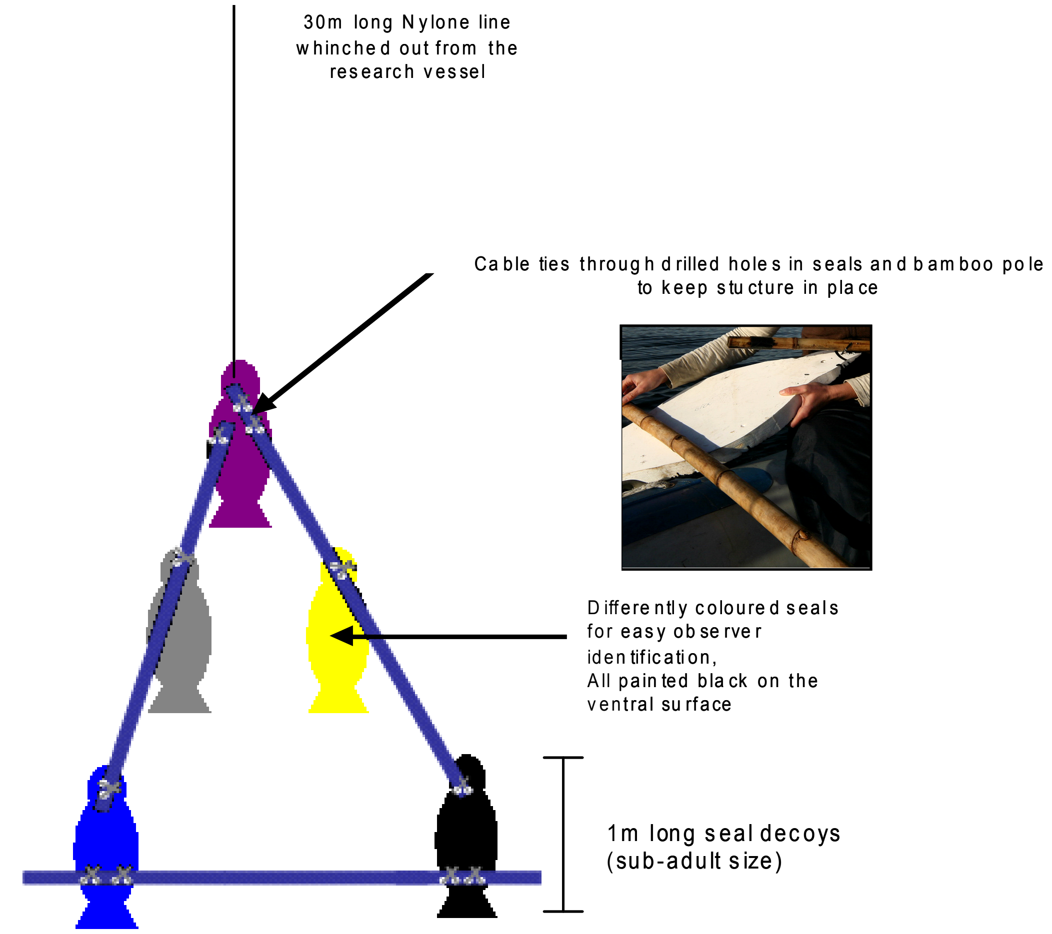
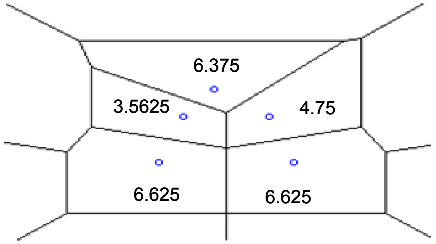
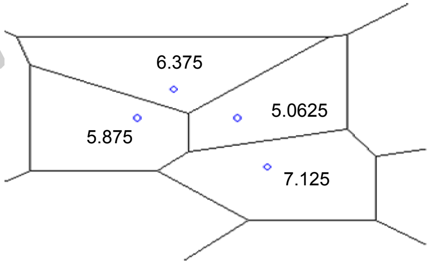
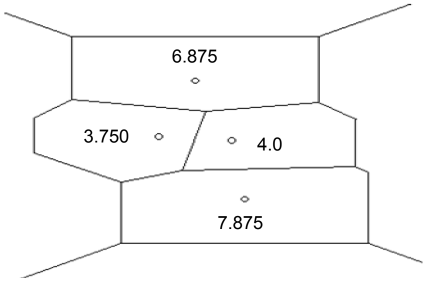




a(i) 5-seal model



a(ii) 4-seal model



a(iii) Real seal group

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Figure 5.1. Experimental apparatus used in the decoy experiments including examples of different group sizes and configurations of seals within artificial groups of decoys. I provide an example of how I estimated the domain of danger for each decoy within the artificial seal group a(i) and a(ii) constructed for experiments in this study, and provide an example of the domains of danger calculated for a real seal group that was randomly selected from observations made from a helicopter a(iii) (see chapter 6).

To reduce the effects of pseudoreplication in predation events, we attempted to identify individual sharks from photographs taken from the boat during each breach attack. Shark size, shape and characteristics associated with dorsal fins are commonly used to identify individual sharks (Domeier and Nasby-Lucas 2007). We managed to obtain 15 photographs from a total of the 36 attacks, six from which we obtained adequate details from the dorsal fin to enable identification. I was further able to use the fixed size of the decoy seals (1m in length) to estimate the following parameters measured from photographs taken of sharks that attacked the decoy rafts (see figure 5.2.):

(i) Tip of snout to anterior side of dorsal fin (TBDL): the length from the tip of the sharks' snout to the anterior side of the dorsal fin. Two sharks were considered distinct from one another if the difference between their TBDL exceeded 0.5m.

(ii) Dorsal fin height (DH): the distance from the base of the dorsal fin to its highest point, in straight line. I considered two individuals to be different if the difference between their DH exceeded 20cm.

(iii) Overall length (OL): the maximum distance between the anterior most tip of the sharks' snout and the posterior most tip of the caudal fin, in a straight line. I considered two individuals to be different if their overall length differed by more than 1m.

(iv) Distinctive markings (BM): individual sharks may have distinct colouration and scars that provide reliable information on their individual identity. Given that this study was performed within an eight week period such markings would be unlikely to change and it was thus possible to use them to discern differences between individual sharks.

(v) Sex: white sharks have readily identifiable secondary sexual characteristics (e.g. claspers in males) that enable the reliable assignment of sex to the attacking shark.

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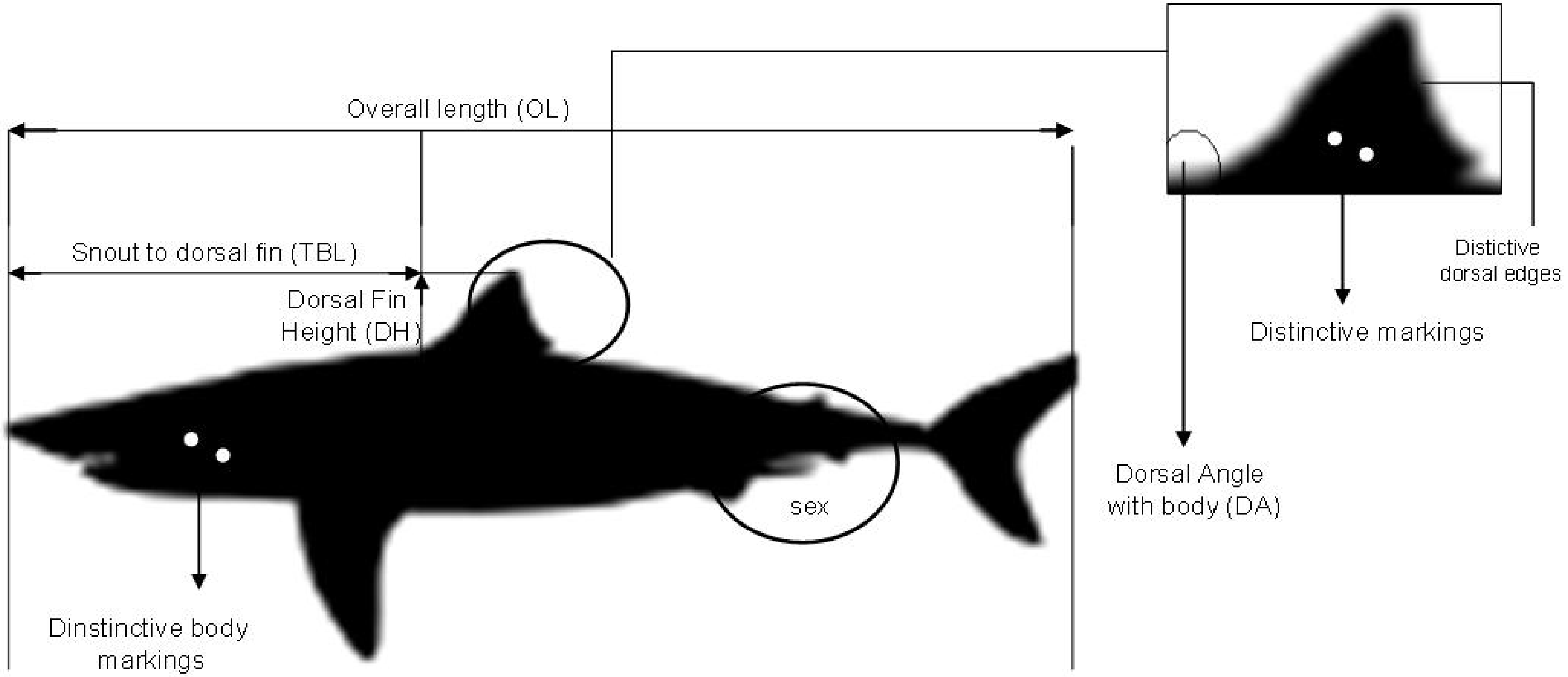

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Figure 5.2. Morphological variables used to identify individual sharks from high resolution digital photographs taken of sharks performing during breach attacks (i.e. airborne) on seal decoys.

Constructing Voronoi tessellations and calculating domains of danger for groups of seal and decoys

Tessellations were constructed by plotting decoy positions as a single point on an x, y grid and using the Voronoi scatter plot function in Stat soft to draw appropriate voronoi diagrams. The area for each individual was calculated by super-imposing 0.25m²x0.25m² cube grids onto the diagrams.

Animal groups are realistically not edgeless, but bounded by either a limited predator attack or predator detection range (James *et al.* 2004). I present results calculated by binding voronoi tessellations with one predator body length, taken as three metres (the average estimated length of white sharks at Seal Island – Kock and Johnson 2006), beyond edge individuals. I assume that predators target individuals within groups and thus will not appear in a space more than one predator body length away from any given individual. To accommodate different suggestions on how to deal with binding group edges, we also calculated "limited domains of dangers" (James *et al.* 2004) (a circular limitation), and bound tessellations with one and two prey body lengths.

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5.3. Results

Are seal groups more compact in areas of high predation risk?

The mean domain of danger was significantly smaller (Wilcoxon matched pairs test, $z=2.028$, $p<0.05$, $n=7$, average group size=10.142 ± 3.836) for seal groups when they were traversing the danger zone (5.051m^2 ±1.680) compared to when they were outside (21.240m^2 ± 8.473) the danger zone (figure 5.3.).

Are larger domains of danger more dangerous?

Attacked decoys had a significantly larger (paired t-test, $\alpha=0.05$, $n=36$, $p<0.001$) domain of danger (mean+s.e.=6.365±0.289 m^2) than the mean of the nearest neighbours domain of danger (5.5.14±0.072 m^2) (Fig 5.4.). Regardless of which method I used to bind the tessellations, or calculate the domain of danger the result remained highly significant (Table 5.2.).

Is predation risk related to a seal decoys domain of danger?

There was a significant positive correlation ($R^2=0.904$, $p<0.001$, $\alpha=0.05$, $n=9$) between the size of the domain of danger and relative predation risk; measured as the proportion of total trials an individual decoy was attacked (Fig 5.5.). The unpredictability and speed of attacks meant that only 15 of the 36 attacks made on the decoy raft were photographed well enough to allow for the subsequent identification of the shark. The combination of variables used to identify individual sharks enabled the positive identification of all 15 sharks that were photographed. Together these data revealed that all 15 sharks were unique (see table 5.2., figure 5.2.). Thus despite not having photographs of all 36 individuals in this experiment, the above result (obtained from what was essentially a random sub-sample) suggests that pseudoreplication was not likely to have had a large effect on the final results.

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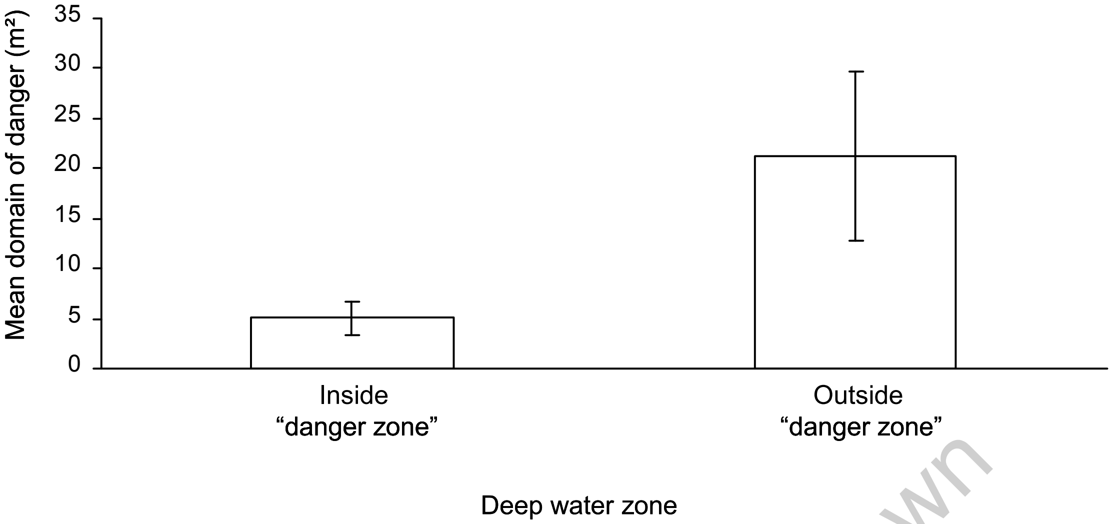

Figure 5.3. The mean domain of danger (m²) of seals travelling in groups as they move from inside to outside the "danger zone" (within the deep water zone) at Seal Island. Error bars represent standard error at the 95% confidence interval.

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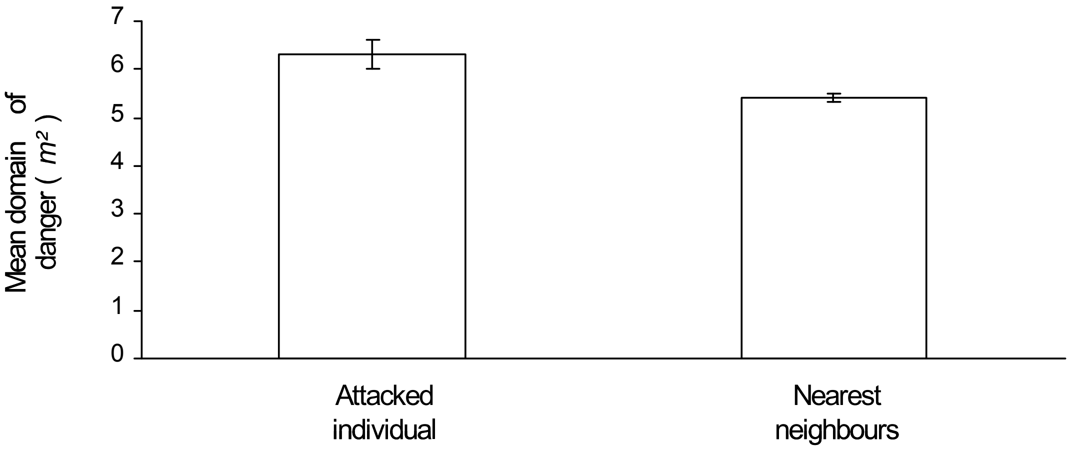

Figure 5.4. Mean domain of danger (m²) of attacked decoys and their nearest neighbours (n=36). Error bars represents the standard error of means at the 95% confidence interval.

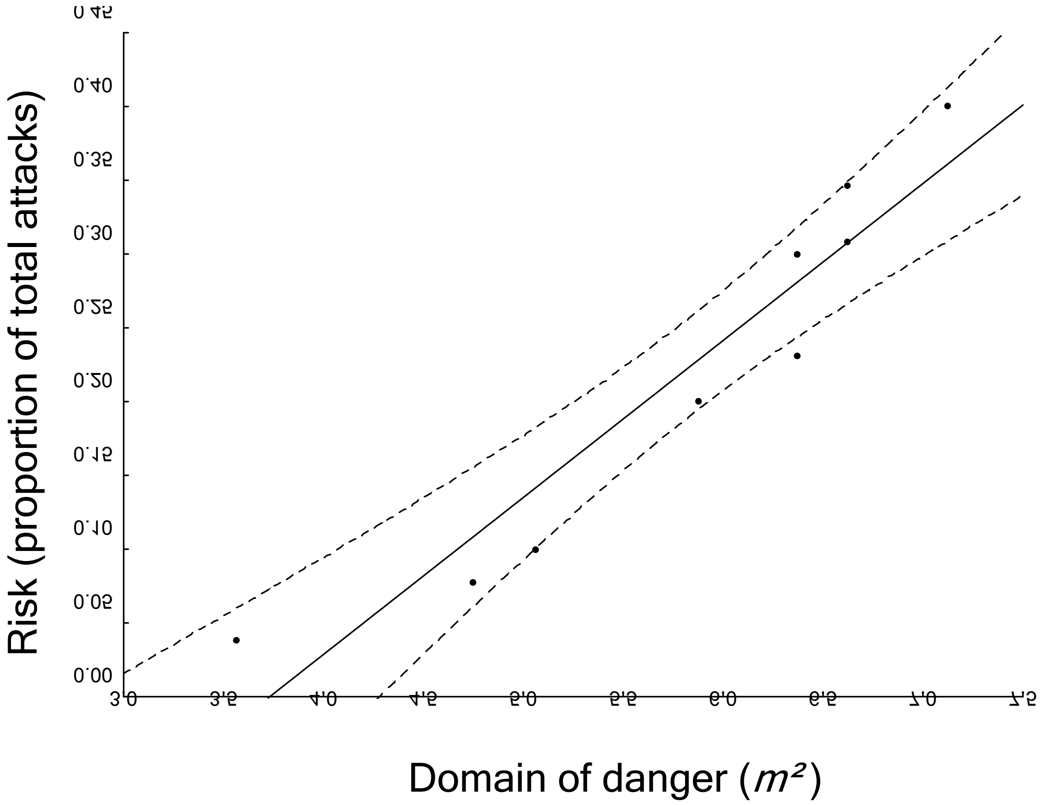

Figure 5.5. The relationship between risk (proportion of total attacks) and the size of the domain of danger (m²). Dashed lines represent the confidence interval at the 95% level.

Table 5.2. Alternative calculations and tests of significance (t-test and linear regression) of the mean Domain of danger (DOD) of attacked versus non-attacked seal decoys. The successive row's of data were calculated by binding groups with one and two prey body lengths, and then by calculating nearest neighbour distance (NND) and limited domains of danger (LDOD) (n=36). Significance is depicted with an asterisk (*).

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	Average DOD of attacked individual (mean±s.e.)	Average DOD of non-attacked individuals (mean±s.e.)	t-statistic	p-value (2 tailed)	Correlation of DOD with risk (R^2 value)	p-value (2-tailed)
1 Prey length	6.684±0.591	6.254±0.216	3.997	0.000315*	0.844	0.0042*
2 Prey lenghts	6.059±0.497	5.601±0.284	4.525	0.000067*	0.8591	0.0003*
NND	1.66±0.307	1.557±0.096	1.602	0.11813	0.243	0.1738
LDOD	7.025±0.141	6.897±0.062	4.284	0.000136*	0.9395	0.00002*

5.4. Discussion

The decoy experiments provided unequivocal support for Hamilton's selfish herd hypothesis. Targeted decoys had a significantly larger domain of danger than the mean of the nearest neighbour's domain of danger, regardless of which method we used to bind the tessellations, or to calculate the domain of danger. This result is of significance because it was possible to standardize the phenotype of the prey, and furthermore, strip the predator-prey system under investigation of the biological complexity that would normally confound the proximate and ultimate selection factors that have lead to the evolution of groups in this species. Complexity between seal-shark interactions is evident at Seal Island with sharks showing a preference seals displaying a range of anti-predator behaviours, including vigilance, to reduce predation risk (Laroche *et al.* 2008).

It was thus imperative to the success of this experiment that we not only controlled for prey phenotype (all prey were identical in size and shape) but prey vigilance too for the latter variable has repeatedly confounded attempts to test the central tenets of the selfish herd hypothesis (Quinn and Creswell 2006, Caro 2005, Viscido and Wethey 2002, Viscido *et al.* 2001 Krause 1994, Fitzgibbon 1990). Sharks attack seals by surprise, with about a 50% success rate (Martin *et al.* 2005, Laroche *et al.* 2008). Of all successful predations, 80% result from a first-time strike (Martin *et al.* 2005). Should a shark fail to capture a seal in the first instance, its' chances of success are much diminished. Seals thus have much to gain from detecting a shark prior to an attack.

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The reliance of sharks on the element of surprise to make a successful kill, adds to the biological reality of Hamilton's initial model. Much has been said in the literature about the limited biological realism of Hamilton's model in which a water snake attacks frogs within a pond from below the surface. However there are, in fact, numerous natural systems in which predators attack prey from below by surprise. For example Leopard seals *Hydrurga leptonyx,* attack naive Adélie penguins *Pygoscelis adeliae* when they enter the water for the first time (Ainsley *et al.* 1985, Hall-Aspland *et al.* 2004), Goliath tiger fish *Hydrocynus vittialis* attack a variety of aquatic organisms from below (Jackson 1961) and Cape fur seals attack cape gannets *Morus capensis* from below when they are resting on the ocean surface (Makhado *et al.* 2006, Crawford and Cooper 1996). It remains to be seen whether these predator-prey interactions will lend themselves to studies that aim to test the selfish herd hypothesis.

Real seal groups are seldom attacked relative to single seals (Laroche *et al.* 2008) suggesting that there are distinct advantages to traversing the danger zone within a group. The presence of single seals within the danger zone reflects the lack of any safe area for single seals that are returning to the island to congregate and form groups prior to traversing the danger zone (see chapter three). Importantly though when seals leave the island and traverse the danger zone they chose to do within a group that can be formed in the safety of shallow water around the island. Although my results corroborate the selfish herd as a plausible mechanism by which grouping could have evolved, the same system illustrates why it could not act in isolation. Animals need at least loose approximation to each other for this mechanism to be part of their behavioural repertoire to reduce predation risk. Thus individuals have to associate from random encounter, before the selfish herd behaviour can shape and regulate group size and geometry.

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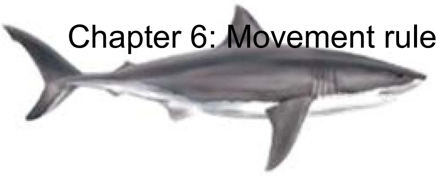
Overall, my results provide evidence that groups are driven by predation risk and that individual spacing within seal groups' influences predation risk by white sharks. My results suggest that the selfish herd hypothesis may be a plausible theoretical framework for explaining the evolution of gregarious behaviour in other similar systems. I provide empirical evidence that the domain of danger is a biologically real spatial construct of differential predation risk (and thus a real entity for natural selection to operate on) and thus authenticate the selfish herd as more than a "theoretical curiosity" (Viscido 2003).



Chapter 6

Movement rules

Do seals move like simple or complex selfish herds?

Abstract

The selfish herd hypothesis is one of the most popular explanations for how animals under predation risk behave to form compact groups. The hypothesis predicts that animals can reduce their own predation risk by moving towards neighbouring individuals and in doing so, decrease the probability of being a victim of a randomly appearing predator. However, many computer simulation studies have found that smaller herds result when animals follow these simple rules and not large, compact aggregations. Although more complex rules can produce large compact groups, the concern is that these rules may be too complex for real animals to follow. Despite much theoretical work, and the selfish herd's popularity, Hamilton's (1971) predictions on how animals should move, and whether this movement results in decrease in risk (as measured by the size of an individual's domain of danger), has all but gone untested in natural systems. Here I analyze the behaviour of individual seals within seven Cape fur seal groups as they move from an area of high to low predation risk. My results suggest that seal behaviour within groups can best be explained by simple rules (movement towards nearest neighbours in time), rather than complex averaging rules. I also show that following these rules results in a decrease in individual domains of danger, and an overall increase in group compactness when the groups are within the high risk area. Conversely, I show that individuals stop approaching their neighbours in areas where predation risk is low, which leads to a decrease in group compaction. My results provide empirical support for the predictions of the selfish herd hypothesis and highlight the importance of environmental constraints on animal decision making.

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6.1. Introduction

Protection from predators is considered to be an important driving force in the development of sociality in many species (Hamner and Parrish 1997, Bednekoff and Lima 1998a, 2004, Lima *et al.* 1999). One popular explanation for how grouping may have evolved in response to predation is the selfish herd hypothesis (Hamilton (1971), an individual-based model that explains (see introduction of Chapter 5 for detailed description) how differential risk amongst previously ungrouped, loosely associated prey individuals could drive the evolution of groups (Hamilton 1971).

Numerous studies (e.g. Parrish 1989, Heard 1992, Ens *et al.* 1993, Watt *et al.,* 1997, Spieler and Linsenmair 1999, Viscido and Wethey 2002) have shown that animal groups collapse towards their centre of mass during and after a predator attack. Group compaction is thought to be the result of individuals within the group attempting to to reduce their domains of danger thus satisfying a central prediction of Hamilton's (1971) selfish herd hypothesis.However, many computer simulation studies have failed to derive large, tight aggregations resulting from animals moving as predicted by Hamilton's hypothesis (Morton *et al.* 1994, Viscido 2003, Morrell and James 2008). Hamilton himself found that a rule of approaching the nearest neighbour does not result in large, dense aggregations (Hamilton 1971), a phenomena he proposed was remedied by groups seeing the collective benefit of moving towards other groups.

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Many subsequent studies have proposed such "collective" assessment rules (Morton *et al.* 1994, James *et al.* 2004, Reluga and Viscido 2005) but these rules have often been criticized as being too complicated for animals to follow in real life situations (Morell and James 2009, Reluga and Viscido 2005). The search for a movement rule that can satisfy both simulated central compaction which can then be verified within a natural system has been referred to as the "dilemma of the selfish herd" (Viscido 2003, Reluga and Viscido 2005).

Research on movement rules in selfish herds has, with the exception of a single study on small fish (Krause and Tegeder 1994), been limited to computer simulations. Most studies have tested a number of alternative rules, under the broad theme of simple and complex rules (Krause and Tegeder 1994, Morton *et al.* 1994, Viscido *et al.* 2002, Viscido and Wethey 2002, Morrell and James 2008). Simple rules apply when animals only identify one or two nearest neighbours and move in their direction, whereas animals following complex rules utilise information on the position of multiple other individuals.

Two simple rules have received the most attention in simulation studies. Firstly, moving towards a nearest neighbour in space (Hamilton 1971, Viscido *et al.* 2002, Morell and James 2009), and secondly moving towards a nearest neighbour in time (Krause and Tegeder 1994). In the latter, the time it takes for an individual to turn towards a nearest neighbour is recorded in addition to the spatial distance between the two individuals.

Averaging rules considered to date have been relatively uncomplicated modifications of simple nearest neighbour rules, where animals move into the space between two nearest neighbours (Hamilton 1971), or more complex rules where animals move towards multiple (two, three and five have been considered) nearest neighbours in space (Morton *et al.*1994, Viscido *et al.* 2002, Morell and James 2009). One more sophisticated addition was the proposal of the local crowded horizon rule (Viscido *et al.* 2002). This rule is based on an animal's perception of its group members, where an animal's movement decision is dependent on many different neighbours, but with weighted importance with distance from neighbour.

The scientific community has not achieved consensus on an optimum movement rule, where optimum is defined by a decrease in average domains of danger of group individuals given the ability of all animals in a group to follow a specific rule (Viscido 2002). Morton *et al.* (1994) showed that moving towards a nearest neighbour (a simple rule) represented a significant improvement to random movement, but that when simulated, individuals typically included more neighbours into their assessment of risk, suggesting that a more complex rule would carry greater benefits. Viscido *et al.* (2002) showed that the most complex averaging rules produced the densest aggregations, therefore, the highest decrease in predation risk. In these studies complex rules appear to be more advantageous than simple or optimal target rules in producing aggregations of animals. Other studies have

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however, shown that following simple rules (which are thought to be more realistic) may result in the formation of large groups (Krause and Tegeder 1994).

Many results suggest that multiple movement rules may be drivers of aggregation, and that specific rules may be more beneficial under different environmental conditions. Wood and Ackland (2007) found that flock dynamics, the size and density of a group, and ecological variables all had a significant effect on which movement rules were most beneficial in producing compact aggregations. Similarly, Morrell and James (2008) showed that complex rules are most successful at reducing risk in small, compact groups, whereas simpler rules are most successful in larger, low-density groups, and when predators attack quickly after being detected by their prey.

Whilst all this theoretical work has focused on the exact selfish herd movement rules, the critical underlying assumptions of the selfish herd hypothesis and empirical evaluation of the predictions based thereon have been largely neglected (Viscido 2003, but see Krause and Tegeder 1994, Quinn and Cresswell 2006).

In the previous chapter (Chapter 5) I provided strong evidence in support of the selfish herd hypothesis. More specifically I showed that white sharks target seals in a group at random, leaving individuals with larger domains of danger more at risk than those with smaller domains of danger. Furthermore, I showed in chapter three that individuals within groups change their position relative to neighbouring individuals (i.e. they jostle), and that they do so in response to heightened predation risk. Clearly this system provides an ideal one in which to investigate movement rules within the theoretical framework of the selfish herd hypothesis, viz., that individuals move towards their nearest neighbours (or in a modification to this rule) to selfishly reduce their domains of danger.

In this chapter I thus investigate:

(a) The general prediction of the selfish herd hypothesis that animals approaching their nearest neighbours reduce their domain of danger. I test this prediction under conditions of high and low predation risk.

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(b) The movement rule, or combination of movement rules (largely following Morrell and James 2008), that best explains movement patterns within seal herds at Seal Island during periods of high predation risk..

(c) Whether the movement rule(s) in b) result in a reduction in the size of the individuals' domain of danger.

I concern myself with proximate consequences of different movement rules, not ultimate questions about how they evolved and spread through populations. I do not explore all possible rules that animals could follow, and acknowledge that these results present only the consequences of local rules. As different rules may sometimes result in an animal moving in the same vector direction, and it is not possible to assess intent, the rules identified are not mutually exclusive from one another. Rather I hoped to, at the very least, deduce whether seals use simple versus complex rules, to reduce predation risk from white sharks at Seal Island.

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6.2. Methods

6.2.1. Study site

I collected behavioural data at Seal Island in False Bay, South Africa (as described in chapter two) during the high predation winter season, both inside and outside the danger zone.

6.2.2. Aerial data collection

To answer questions on the spatial geometry of the seal groups leaving Seal Island, we followed seven independent groups of seals (77 individuals, in groups of 3 – 21) using a light helicopter. Seal groups were filmed with a handheld digital camera from the moment they left thet safe shallow waters on the south sideof the island for a distance of approximately two kilometres from the island. The duration and route traversed by the group was recorded with a handheld GPS (Garmin e-trex). Southwell (2005) found that a helicopter flying directly over and lower than 130m altitude had no effect on the behaviour of three species of pinnipeds and two species of Penguins. A similar result was obtained for this study and the seals appeared to be unaware of the helicopter unless the shadow of the aircraft passed directly over them. Shadows elicited classical anti-predator behaviour (a rapid change in movement patterns of affected seals) and these events were thus excluded from the subsequent analyses on group geometry, and behaviour. For the most part I simply requested that the pilot avoids casting a shadow on the group to exclude any observer effects on the seal group(s) under observation.

Aerial follows were subsequently analyzed using video software (Moviemaker) to freeze-frame groups and estimate distances between seals. Adult female seals are on average 136±14.112 cm in length and were thus used as the metric upon which other measurements within the group (e.g. distances between individuals) could be estimated. Although there might be some error contingent upon using this measure it is important to bear in mind that a paired statistical evaluation of group geometries was used and thus the comparisons were between the same individuals inside and outside the high predation risk area (i.e. the danger zone). I calculated domains of danger, described in more detail below, and compared average domains of danger inside versus outside the danger zone, before and after movement rules.

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6.2.3. Constructing voronoi tessellations

Tessellations were constructed by plotting seal positions as a single point on an x, y grid and using the Voronoi scatter plot function in Stat soft to draw appropriate voronoi diagrams. In the simplest case of a voronoi diagram (also known as a Dirichlet tessellation), we are given a set of points *s* in the plane. Each site *s* has a voronoi cell, consisting of all points closer to s than to any othe sites (Okabe *et al.* 1992).

The area around each individuals was calculated by super-imposing $0.25\text{m}^2\text{x}0.25\text{m}^2$ cube grids onto the diagrams and summing the grids. Seal groups are not edgeless, but bounded by either a limited predator attack or predator detection range (James *et al.* 2004). I present results calculated by binding voronoi tessellations with one predator body length, taken as three metres beyond edge individuals (the average estimated length of white sharks at Seal Island – Kock and Johnson 2006). I assume that predators target individuals within groups and thus will not appear in a space more than one predator body length away from any given individual.

6.2.4. Analysis of movement rules

To assess which theoretical movement rules (as shown in table 6.1.) best predicted real seal movement relative to neighbouring individuals, I used the freeze-framed function in the software package Moviemaker, to estimatethe size of individual seals and their domain of danger (as described above). For every focal individual, I identified the neighbours in accordance with the movement rule under investigation, as detailed below (table 6.1.).

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Table 6.1. A list of the simple and complex movement rules investigated in this study. The author(s) of each and the predictions to satisfy the rule(s) are detailed.

Rule	Proposed by	Prediction
Simple Rules		
Nearest Neighbour	Hamilton (1971)	An Individual moves toward the nearest individual in space
Time minimization	Krause and Tegeder (1994	An individual moves toward the nearest individual in time (takes account of the time taken in turning towards a neigbour).
Hamiltonian	Hamilton (1971)	An individual moves into the space between its two nearest neighbours.
Hamiltonian in time	Modification of Hamilton (1971)	An indiviudals moves into the space between its two nearest neighbours in time.
Complex rules		
n closest neighbours	Morton *et al.* (1994)	An individual moves toward the average location of several (n) nearest neighbours. I investigate three nearest neighbours.
n closest neighbours in time	Modification of Morton *et al.* (1994)	An individual moves toward the average location of three nearest neighbours in time.
Local crowded horizon	Viscido *et al.* (2002)	An individual moves towards the area with the densest concentration of con-specifics. The influence of neighbours on the focal animal varies with the distance of the neigbours relative to the focal individual. I use the perception function:$f(x)=1/(1+kx)$, where x is the distance from the focal individual and k=0.375 as suggested by Viscido *et al.* (2002) and Morell and James (2009). Thus, individuals close to the focal individual have a strong influence on movement direction, whereas distant group members exert a much weaker influence. I only considered individuals in front of focal individuals in this analysis.
Non-selfish herd rules		
Forward trajectory	Modification of random movement rule, e.g. Viscido *et al.* 2002	An individual moves in a forward trajectory and does not approach any neighbouring individual.
Group centre	This study	An individual moves toward the centre axis of the group.

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Video footage of all seals swimming within each group was analysed once the group was at leasy 500m from the island. Each time a given rule was followed by an individual in the group it was given a score of one (1), whilst all the other rules were given a score of zero (0). Where an individual followed more than one rule, both, or all rules followed were allocated a score of one (1). I repeated this analysis for each individual outside the danger zone. Lastly, I calculated the domain of danger prior to and after a movement rule was performed for each focal individual.

Each individual was marked in an initial freeze-frame of the group, and movement for each individual within that group scored three different times. This was repeated for every (independent) individual in the seven groups followed. The average of each individual's scores contributed one data point to the average.

6.2.5. Group size and density

To calculate group size I counted the number of seals observed within the group at a random point ca. 500m from the island. Two of the seven study groups fissioned into two smaller groups subsequent to this count. I used the pre-fission count as the group size estimate in both cases. All movement rule analyses were conducted prior to fisioning for both groups.

Group density was measured as the mean of all the individual domains of danger within a group. I used group density from the point at which movement rules were assessed in all seven groups (and thus the density which informed the movement rule results).

6.2.6. Statistical analyses

I performed exploratory descriptive statistics prior to running all statistical tests to test relevant assumptions of normality of distributions, homogeneity of variances, independence, linearity and co-linearity of variables.

If data were normal or could be transformed to normality, parametric statistics were used following Keogh and Quinn (2003). In all other cases I used the robust rank-based non-parametric equivalents following Wilcox (2003). To analyze two sample datasets

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(all datasets were paired) I employed paired t-tests and non-parametric Wilcoxon paired tests. In instances where a single categorical variable predicted a continuous response variable I employed single factor ANOVA's or a non-parametric Kruskal-Wallis 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. To test differences between observed proportions I employed the Cochran's Q test for assessing matched proportions.

To analyze the relationship effect of group size on density, I employed a general linear model (GLM), after satisfying the assumptions of a normally distributed response variable. To assess the interaction between complex, simple and forward trajectory rules and group density, I employed a generalized linear model (GLMM). The response term for this analysis (following of movement rule=1, not following the movement rule=0) was binary, necessitating the use of a logit link-function to correct for unknown error terms. Estimators were fitted using Grauss-Hermit approximations (as there were very few random effects) and stepwise regression was not required as there was no co-linearity between variables (group size was not included in the model). I use the Wald-F statistic to draw statistical inferences.

All statistical tests are two-tailed. Parametric means are given with standard errors of the mean and rank-based values of locations with standard errors of the median (Wilcox 2003).

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6.3. Results

Can the selfish herd movement rules explain seal behaviour within groups?

There was significant variation in the proportion of seal movement (Cochran Q test, Q=69.464, df=8, $p<0.001$) that could be explained by different movement rules. The "nearest neighbour in time" and the "Hamiltonian in time" rules described 54.29% (Cochran Q=7.692, $p<0.01$) and 62.83% (Cochran Q=11.267, $p<0.001$) of all movement vectors. Other movement rules described between 9% and 38.46% of all movement vectors with "front trajectory movement" and "group centre" rules describing 23.28% and 25.71%, respectively. Outside the danger zone, the "forward trajectory rule" could explain 82.14% of all seal movement, significantly more (Cochran Q=143.946, $p<0.001$) than any other movement rule (<14.44%) (figure 6.1.).

Seals following selfish herd rules had a significantly smaller domain of danger (all paired tests are Wilcoxon matched paired t-tests) than before the rule was followed. Individuals whose behaviour was best described by the nearest neighbour rule decreased their domains of danger (DOD) significantly from a mean±s.e. of 3.362±1.236 to 2.122±1.236m^2 (z=2.241, n=21, $p<0.05$). Significant reductions in the DOD were also recorded for seals following nearest neighbour in time (2.672±1.211 to 1.654±0.922m^2;z=3.603, n=38, $p<0.001$), Hamiltonian (2.167±1.396 to 0.751±0.795m^2; z=3.636, n=18, $p<0.001$), Hamiltonian in time (1.44±0.633 to 0.887±0.426m^2; z=3.034, n=24, $p<0.01$), three nearest neighbours (1.910±1.488 to 0.460±0.427m^2; z=2.366, n=7, $p<0.01$), three nearest neighbours in time (1.488±0.765 to 0.476±0.262m^2; z=3.206, n=16, $p<0.01$). Individuals whose behaviour could be described by a forward trajectory movement rule had significantly larger (Wilcoxon matched pairs test, z=2.45, n=18, $p<0.05$) domains of danger (1.694±1.799 vs. 3.334±4.078m^2) after following this rule (figure 6.2.).

There was significant variation in the magnitude of the change in the size of the domain of danger (Kruskal-Wallis, H=29.017, p=0.0012) associated with the different movement rules. Most movement rules, with the exception of the "group centre",

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rules reduced average domains of danger significantly more (multiple comparison of mean ranks, all $p<0.028$) than front trajectory movement rules (figure 6.3.).

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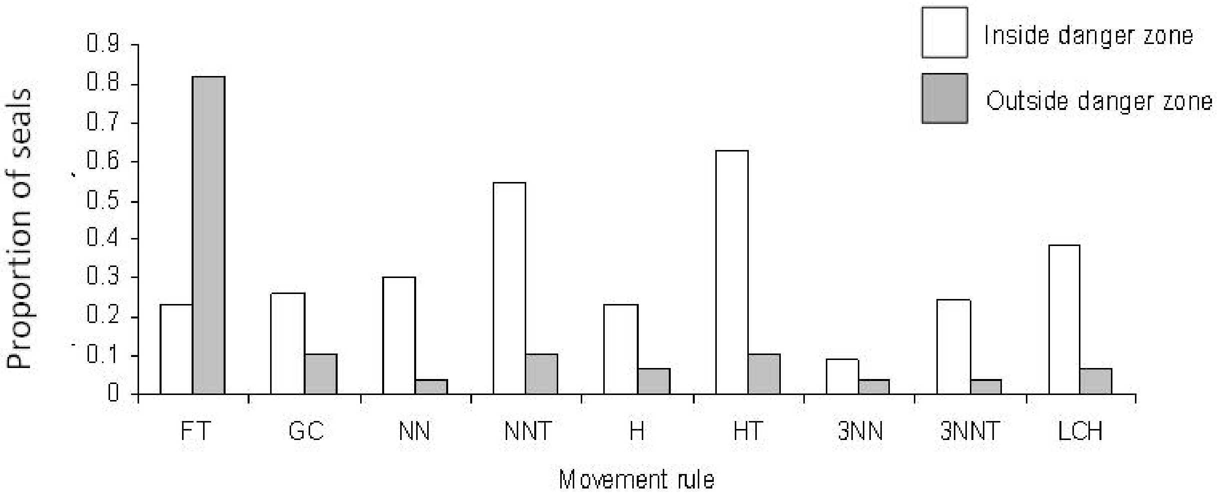

Figure 6.1. The proportion of seals whose movement could be described by different movement rules, inside (white bars) and outside (grey bars) the danger zone. I consider the front trajectory rule (FT) and the group centre (GC) rules as rules against which selfish herd moment can be judged. I consider the nearest neighbour in space (NN) and time (NNT), the Hamiltonian in space (H) and time (HT), three nearest neighbours in space (3NN) and time (3NNT) and the local crowded horizon rule (LCH). It is important to note that rules are not mutually exclusive, and that proportions do not add up to 1.

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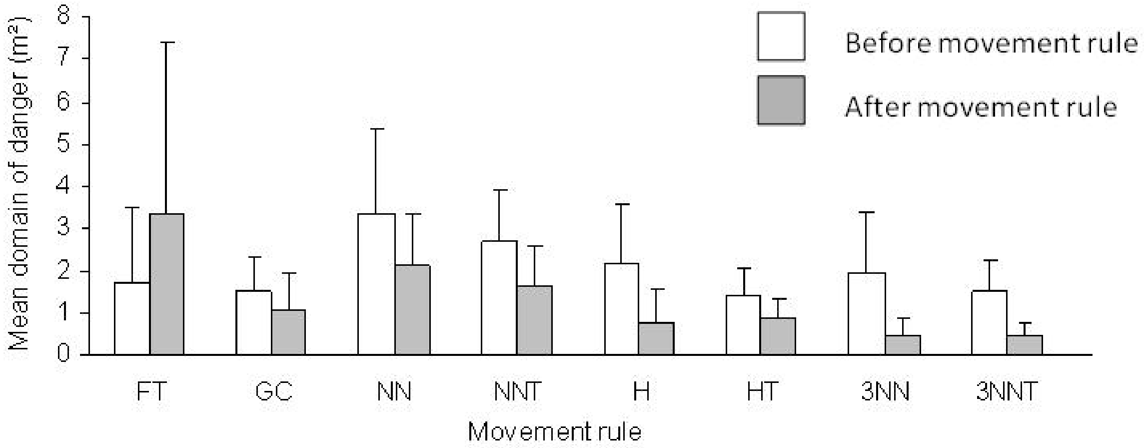

Figure 6.2. The mean domain of danger of seals before and after following a specific movement rule. Movement rules assessed are the front trajectory rule (FT), the group centre rule (GC), the nearest neighbour in space (NN), nearest neighbour in time (NNT), Hamiltonian in space (H) and time (HT), three neighbours in space (3NN) and time (3NNT) rules, and the local crowded horizon (LCH) rule. Error bars represent standard error at the 95% confidence interval.

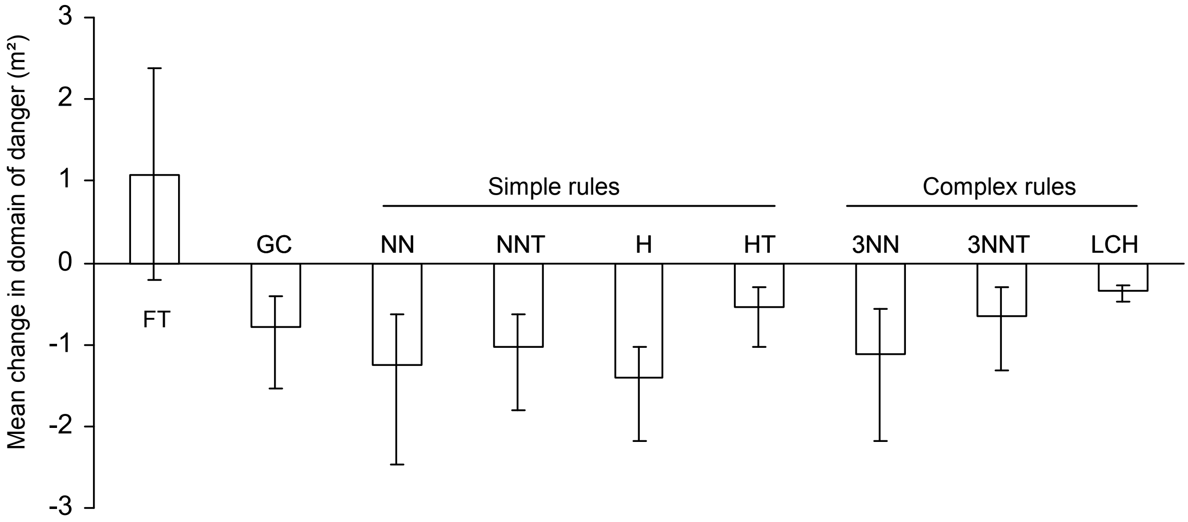

Figure 6.3. The mean change in the magnitude of the domain of danger associated with different movement rules. Error bars represent standard error at the 95% confidence level. The forward trajectory (FT), group centre (GC), nearest neighbour (NN), nearest neighbour time (NNT), Hamiltonian (H), Hamiltonian in time (HT), three nearest neighbours (3NN), three nearest neighbours in time (3NNT) and local crowded horizon (LCH) rules are shown.

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Do simple or complex rules in space or time best explain seal movement?

Rules where animals consider their nearest neighbours in time explained a significantly larger proportion of seal behaviour (Cochran Q =26.1.33, p<0.001 for simple rules, Q=16.2., p<0.0001 for complex rules) than those where animals considered their nearest neighbours in space (77.93% vs. 41.56% for simple rules, 46.7.5% vs. 23.37% for complex rules). Movement rules where animals did not consider specific neighbours but just aimed for the group mid-line only explained 23.38% of seal movement, which was no different from the “front trajectory” rule (also 23.38%). Simple rules in time could, in turn, explain significantly more seal movement (Cochran Q=24, n=77, p<0.001) than complex rules in time (77.92 vs. 46.7.5%).

Although there was significant variation in the mean change of individual domains of danger (Kruskal Wallis H=25.412, p=0.001) associated with different movement rules, there were no significant differences (multiple comparison of mean ranks, p>0.1) between rules of different complexities, or rules that considered nearest neighbours in time and those that considered nearest neighbours in space. The forward trajectory rule was, however, less successful at reducing domains of danger than all selfish herd rules (multiple comparison of mean ranks, p<0.01), but there was no significant difference between this rule and the group centre rule (figure 6.5.).

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The effect of group size and density

Group densities were significantly lower ($F_{1,7=}$ 0.306, p=0.024) at smaller group sizes (table 6.2.). There was a significant effect of group density (Wald F=6.040, p<0.05) and movement rule (Wald F=27.206, p<0.00001) on the probability of seal movement. There was also a significant interaction between group density and movement rule (Wald F=6.8.61, p<0.05). I found that whilst there was a significant interaction for group density and complex rules (Wald F=6.8.06, p<0.01; complex rules could describe more group movement at higher densities), there was no significant effect of the interaction between group density and simple rules, or group density and forward trajectory rules on the model (Table 6.3.).

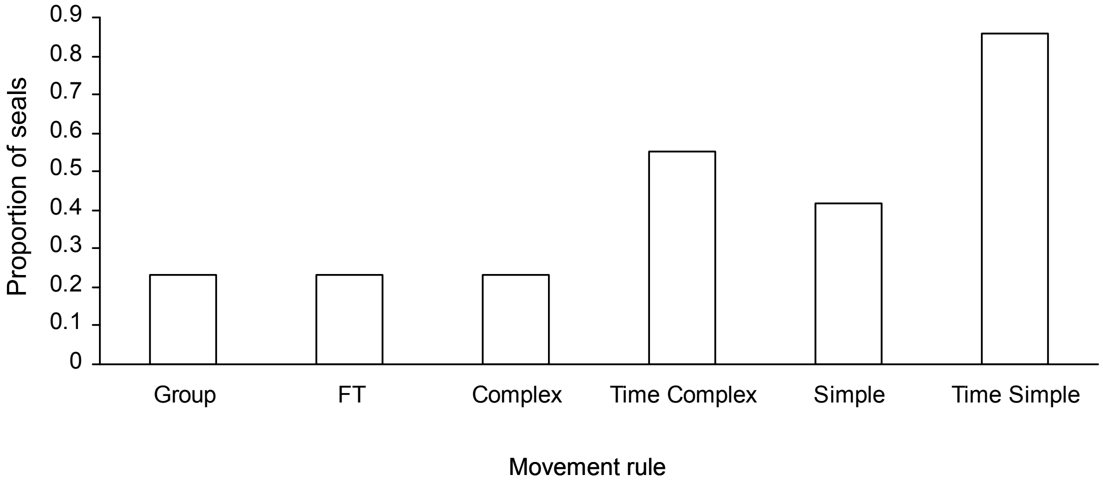

Figure 6.4. The proportion of seals whose behaviour could be explained by complex and simple selfish herd rules in space (simple and complex) and time (time complex and time simple), compared to simple dilution rules (group) and forward trajectory rules (FT).

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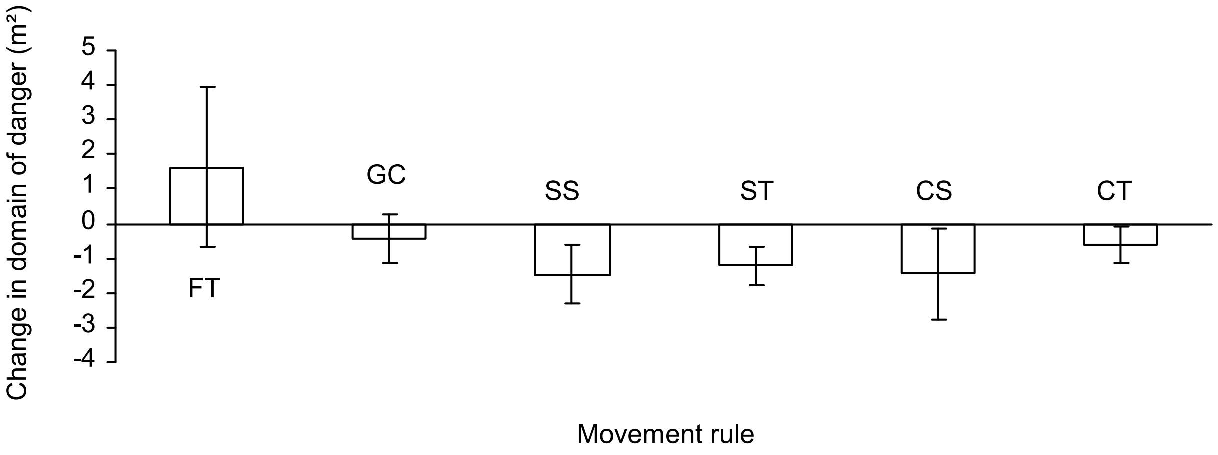

Figure 6.5. Change in the mean domain of danger associated with different movement rules. The x-axis shows the forward trajectory rule (FT), the group centre rule (GC), complex rules in space (3NN) and time (3NN, LCH), and simple rules in space (NN, H) and time (NNT, HT).

Table 6.2. General linear model of the effect of group size on group density (as measured by mean domain of danger in m²), (n=7, r²=67.33%). Table shows parameter estimates (Effect), standard errors (SE), associated test statistic (F), and significance (p-value).

Model term	Effect	df	F	SE	p
Intercept	180.024	1.000	28.042	6.420	0.003
Group size	66.158	1.000	10.306	6.420	0.024

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Table 6.3. The effect of movement rule, density and simple, complex or forward trajectory rules on predicting seal movement. The table shows a GLMM analysis with a binomial error structure and a logit link. Parameter estimates (estimate), standard errors (SE), associated test statistic (Wald statistic, and significance (p-value) are listed for each model term.

Model term	Estimate	df	Wald	SE	p
Movement Rules	0.902	1.000	27.206	0.326	0.000001
Density	-0.121	1.000	6.040	0.049	0.013985
Rule*Density		2.000	6.861	0.068	0.032368
Simple*Density	0.078	1.000	2.590	0.069	0.248226
Complex*Density	-0.189	1.000	6.806	0.073	0.009087
FT*Density	0.111	1.000	2.590	0.068	0.107539
Intercept	0.512	1.000	5.119	0.226	0.023668

There was no significant variation in the mean length of seals (one-way ANOVA, F=1.084, p=0.381) in the different seal groups. Similarly, there was no significant differences between the mean size (student t-test, p>0.5) of the leading individuals (114.380 ± 2.355cm, n=20) and the mean of all seals in the group (113.285 ± 4.585cm, n=77). In this analysis, the seals that were at the front of groups at the time of the snapshots were considered as “leading individuals”. In some groups there was no discernable distance between individuals, and so multiple individuals within single groups were included as “leading” animals.

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6.4. Discussion

The selfish herd hypothesis is a popular explanation for how groups may arise from selfish individual behaviour (Morton *et al.* 1994, Viscido 2003). The hypothesis predicts that compact groups will result if all individuals move towards other individuals in their immediate environment, but exactly how this is achieved has been the subject of much theoretical debate. The problem stems from the fact that simple movement rules, as originally proposed by Hamilton (1971), do not seem to produce large compact groups, but rather smaller clusters, whilst complex rules may be too difficult for animals to follow in real systems (Viscido *et al.* 2002, Morrell and James 2008). Theoretical arguments for the resolution of “selfish herd” rules have proliferated but empirical verification has been lacking (Viscido 2003). In this study I provide data on movement rules and use the results to shed light on the “dilemma of the selfish herd” (Viscido 2003, Reluga and Viscido 2005).

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Firstly, I provide support for the predictions of the SHH by showing that selfish herd rules can explain individual seal movement better than forward trajectory rules (i.e. individuals do not approach neighbouring individuals), and that these movement rules are, on average, associated with reduced domains of danger for individuals inside a zone of high predation risk. Moreover, selfish herd rules explained only 14% of seal movement vectors outside this “danger zone”, an area associated with low predation risk, and low group compaction (see chapters three and five). Additionally, the rule that seals should move toward the centre of the group did not describe individual movement any more than the forward trajectory rule (figure 6.2., 6.3.). Together these results suggest that seals have evolved movement rules that conform to the predictions of the selfish herd hypothesis (Foster and Terherne 1981, Turner and Pitcher 1986).

These results are particularly important as they follow on directly from the empirical validation of the critical prediction of the SHH, namely, that an individual’s domain of danger is proportional to its relative predation risk (see chapter five). It also informs earlier behavioural results at this island (chapter three) that showed that seals jostled in groups (changing position relative to other seals) within the danger zone during winter when sharks are abundant, but not during summer when there are few sharks, and furthermore that seals did not jostle once they were outside the danger zone during either season.

Analysis of movement patterns within groups suggests that seals at Seal Island are using simple movement rules to reduce predation risk. Seals either moved towards their nearest neighbours or in the way that Hamilton (1971) first proposed, into the spaces between two neighbouring individuals. In accordance with Krause and Tedgeder's (1994) findings on stickleback fish, I found that rules where individuals considered nearest neighbours in time, rather than in space, offered a better explanation for seal movement within the danger zone. This is to be expected given that individuals are unlikely to move towards a neighbour that is nearest to it spatially, but behind them or in the opposite direction to which a group is travelling in.

Although I found no differences in the success of differerent selfish herd rules (see Wood and Ackland 2007, Morrell and James 2008), ecological factors may well provide an explanation for the result that simple rules described more seal behaviour than complex rules (figure 6.4.). For example, limited visibility below water and the porpoising of seals may limit the spatial information that each seal could gather on other group members. Thus, seals may not have adequate information to make complex decisions (based on where it's three neighbours, or the most crowded area of a horizon is). If seals do not have a "crowded horizon" (Viscido *et al.* 2002, Viscido and Relugu 2005) on account of reduced visibility of other group members, this system may not be appropriate for assessing the local crowded horizon rule, or at least requires that a much adjusted perception function be used.

The suggestion that the level of information that individuals have on group members may influence the use of simple or complex movement rules is supported by the results on group size and density (table 6.3. It is important to note here that the sample size for this analysis is very small, n=7). Whereas simple rules could describe more seal movement than complex rules at all group sizes and densities, complex rules performed better at high densities compared to low densities. At higher group densities, individuals may have better information on group members because they are in closer proximity to each other, thus allowing for the use of more complex rules.

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Although this study only provides a snapshot of how real animals move relative to their nearest neighbours, it nevertheless provides a biologically real example of the hypothetical conditions under which the selfish herd was developed (Hamilton 1971). Under these conditions, where the domain of danger is validated as a construct of risk (Chapter 5), where there are no confounding foraging or social- and age-class effects (our results seem to suggest the latter, figure 6.6.), my results show that individuals move towards their nearest neighbours or the spaces between two nearest neighbours to reduce their relative domain of danger, in accordance with the main prediction of the SHH.

However, the "dilemma of the selfish herd" is that simple rules (as predicted by the selfish herd hypothesis) do not seem to result in large, compact groups that are frequently observed in nature. My results show that seals (prey individuals) do follow simple rules and that these rules may reduce an individual's domain of danger and result in compact groups. However, it is important to stress that the mean group size of seals leaving Seal Island is only about ten (chapter five). Furthermore both of the larger groups (give sizes) in this study fissioned into two smaller compact groups once inside the danger zone (*pers. obs.*). Thus similar to the findings of theoretical studies, it would appear that large groups, a phenomenon that the selfish herd is often invoked to explain, cannot be explained by individuals following simple movement rules.

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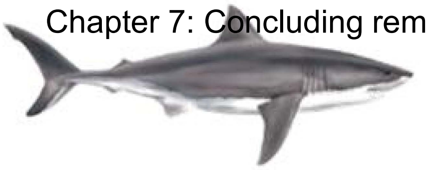
In summary I am cautious about the generality of the findings presented here. More specifically I doubt whether the findings can be extrapolated towards more complex systems where social and foraging factors do play a role, or where individuals have better information on other group members and have access to information on "crowded horizons". Whilst my results provide strong empirical evidence in support of the predictions of the selfish herd hypothesis, they also highlight need to divorce this hypothesis from its "safety-in-numbers" guise and find the appropriate conditions under which it may offer a general explanation for how animals behave in groups.



Chapter 7

Concluding remarks

Avoiding sharks in a landscape of risk

Understanding anti-predator defences represents an important step in understanding and contextualising ecosystems, as predators affect prey populations both lethally and sub-lethally (Lima 1998, Brown *et al.* 2001, Peacor and Werner 2001, Heithaus and Dill 2002, Khan and Ghaleb 2003, Werner and Peacor 2003, Cresswell 2008, Schmitz *et al.* 2004, Preisser *et al.* 2005, Owen-Smith and Mills 2006, Verdolin 2006). Animals may show a great variety of behavioural patterns when threatened by predators, altering behavioural and morphological states, spatial movement and temporal niche use (Magurran and Pitcher 1987, Pitcher and Parrish 1993, Cresswell 2008, Ruxton *et al.* 2004, Caro 2005).

The aim of this thesis was to describe seal spatiotemporal activity and behaviour in relation to a spatially and temporally variable landscape of white shark predation risk. Having described the patterns of seal activity in relation to variable risk (chapter 3) I then tested two hypotheses that are central to predator/prey theory, namely the risk allocation hypothesis (chapter 4) and the selfish herd hypothesis (chapter 5).

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In this final chapter I expand on the context of the landscape of risk at Seal Island within False bay and the contribution of my results to the study of the risk allocation and selfish herd hypotheses, consider these theoretical results in the context of shark/seal predator/prey interactions at Seal Island, and comment on this contribution to the general understanding of predator-prey theory.

Contextualizing the experimental results presented in this thesis

The dynamics of the predator prey relationship between sharks and seals at Seal Island bears a striking resemblance to Hamilton's original thought model. This is fortuitous for many previous studies (see Viscido 2003 for a review) have suggested that the hypothetical example provided by Hamilton was too far removed from reality making it difficult to meet the assumptions when attempting to test the selfish herd hypothesis in real predator prey systems, Importantly there are other predator/prey systems that might also lend themselves to an empirical evaluation of the selfish herd hypothesis.. For example Leopard seals *Hydrurga leptonyx* attack naive Adélie penguins (*Pygoscelis adeliae*) when they enter the water for the first time (Ainsley *et al.* 1985, Hall-Aspland *et al.* 2004), Goliath tiger fish *Hydrocynus vittialis* attack a variety of aquatic organisms from below (Jackson 1961) and Cape fur seals attack paddling cape gannets *Morus capensis* from below the surface (Makhado *et al.* 2006, Crawford and Cooper 1996). There are of course many predator/prey systems for which Hamilton's (1971) model *is* artificial, and empirical tests in systems with distinct edge effects (systems where the selfish herd is often invoked as an explanation) remain an important area of research to establish the generality of the SHH.

Considering how widely the SHH has been cited, the "conditions under which the selfish herd can be invoked to explain grouping behaviour remain surprisingly vague. I attempt to address this below and in figure 7.2., by integrating the predictions and assumptions of the selfish herd with the broader framework within which grouping is understood (see chapter 1).

Why groups form

In chapter one I explained how the costs and benefits of aggregation result in an optimal group size. These costs and benefits relate to the ultimate reasons for grouping including protection from predators, increased access to mates or improved foraging efficiency. The selfish herd hypothesis aims to explain how predation risk might drive the formation of groups and at Seal Island in which there is clear spatiotemporal separation of predation from other drivers of grouping the SHH is clearly an appropriate theory to test. My results revealed clear advantages to group formation with single individuals and individuals in small groups being attacked more frequently than individuals in large groups (≥ 5 individuals) (chapter 3). Within groups the selfish herd hypothesis assumes that a predator appears at the surface and attacks the nearest prey individual from where it appears, which results in each individual within the groups having an area around them within which they are more at risk than any other individual in the group. The size of this area or domain of danger is proportional to an individual's relative predation risk, and thus individuals constantly adjust their relative positions to reduce the size of the domain of danger (explained in detail in chapter 6). The end result of this selfish movement rule is an increase in the compaction of the group under conditions of high predation risk (chapters 5 and 6).

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How groups form

The selfish herd hypothesis could not be used to explain the formation of groups prior to their departure from Seal Island. Groups almost all leave from a single area to the south of the Island known as the “launch pad” (chapter 3). The launch pad is a shelf of shallow water that extends out from the island. Seals aggregate here during the high predation risk winter season prior to leaving in groups. How these groups form at the launch pad remains to be investigated and should probably best be addressed within the framework of self-organization (Rands *et al.* 2003, Rands *et al.* 2004, Couzin and Kruase 2003,Sumpter 2006, Couzin 2007) and/or consensus decision making (Conradt and Roper 2003, 2005, 2009).

Factors that influence how groups can form

The selfish herd hypothesis predicts that animals move towards their nearest neighbours, motivated by the selfish desire to reduce their predation risk. However, a prerequisite is that neighbours are near enough to one another so that individual movement decisions are based on the information available to individuals on the relative position within the group.

Both points bear relevance to our results at Seal Island. In chapter 3 I show that groups probably form as a result of over-dispersing because of food. However, testing the selfish herd requires areas of differential risk within the same group. One needs to demonstrate that groups are more or less compact in accordance with lower or higher predation risk. To achieve compact groups individuals need to have information about their movement relative to other individuals and adjust their behavior accordingly (chapter 6) to reduce their domains of danger (chapter 5). If all members of a group follow similar rules, compact groups will form (chapter 6).

A prerequisite of these movement rules is that individuals can assess their position within the group relative other group members. My results in chapter 6 suggest that the reduced visibility of an aquatic environment means that seals can only use simple rules based on the movement patterns of their nearest neighbours. Importantly, however, these rules suffice for the formation of compact groups and thus seals are capable of reducing their domains of danger within groups in response to heightened predation risk providing support for Hamilton’s selfish herd hypothesis.

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A shortcoming of this study was that I did not compare group compactness in winter with summer, which would have been very useful to further corroborate or refute this statement.

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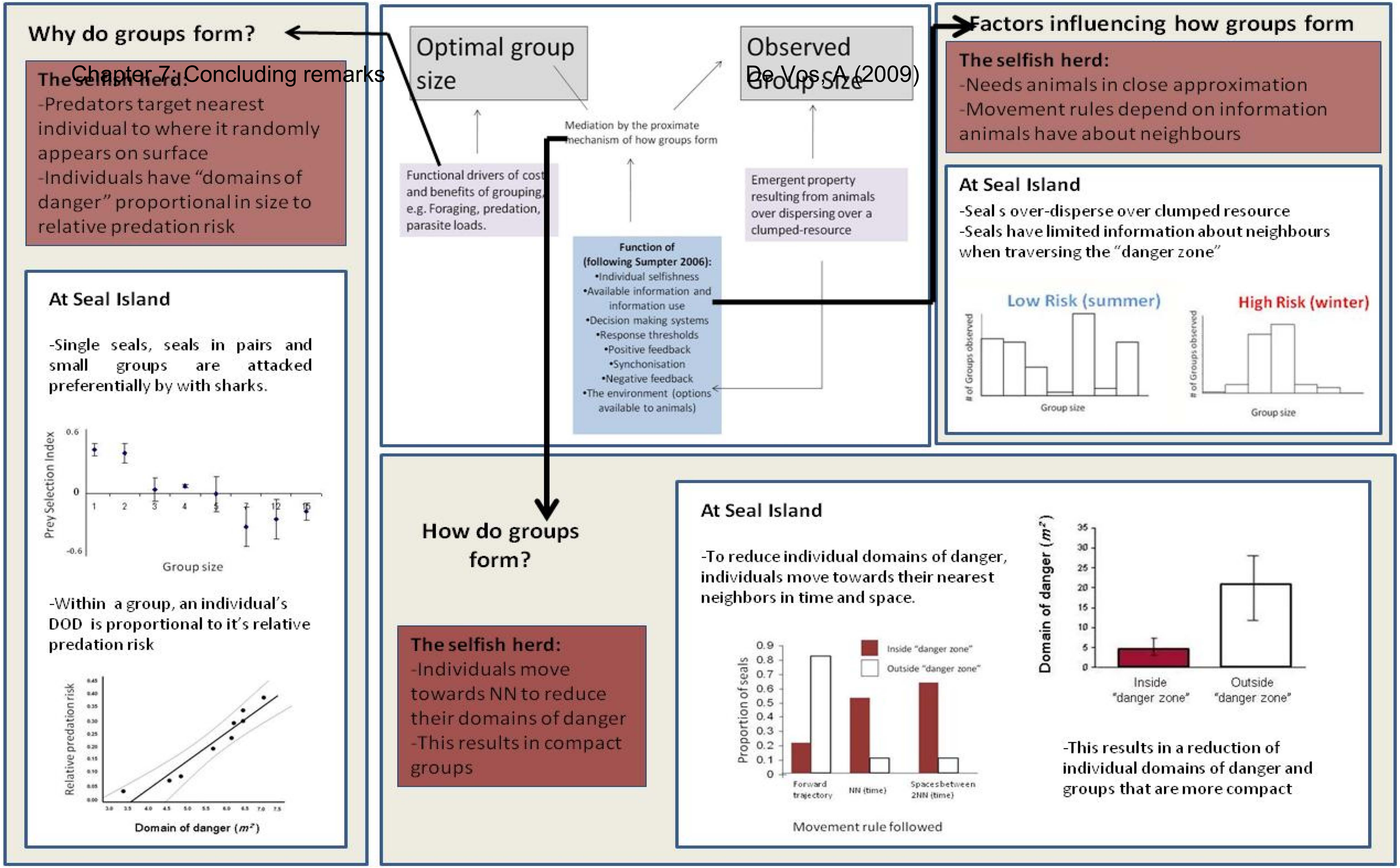


Why do groups form?

The selfish herd:

-Predators target nearest individual to where it randomly appears on surface

-Individuals have "domains of danger" proportional in size to relative predation risk

At Seal Island

-Single seals, seals in pairs and small groups are attacked preferentially by with sharks.

-Within a group, an individual's DOD is proportional to it's relative predation risk

Functional drivers of cost and benefits of grouping, e.g. Foraging, predation, parasite loads.

Function of (following Sumpter 2006):

- Individual selfishness
- Available information and information use
- Decision making systems
- Response thresholds
- Positive feedback
- Synchonisation
- Negative feedback
- The environment (options available to animals)

Emergent property resulting from animals over dispersing over a clumped-resource

Factors influencing how groups form

The selfish herd:

-Needs animals in close approximation

-Movement rules depend on information animals have about neighbours

At Seal Island

-Seal s over-disperse over clumped resource

-Seals have limited information about neighbours when traversing the "danger zone"

How do groups form?

The selfish herd:

-Individuals move towards NN to reduce their domains of danger

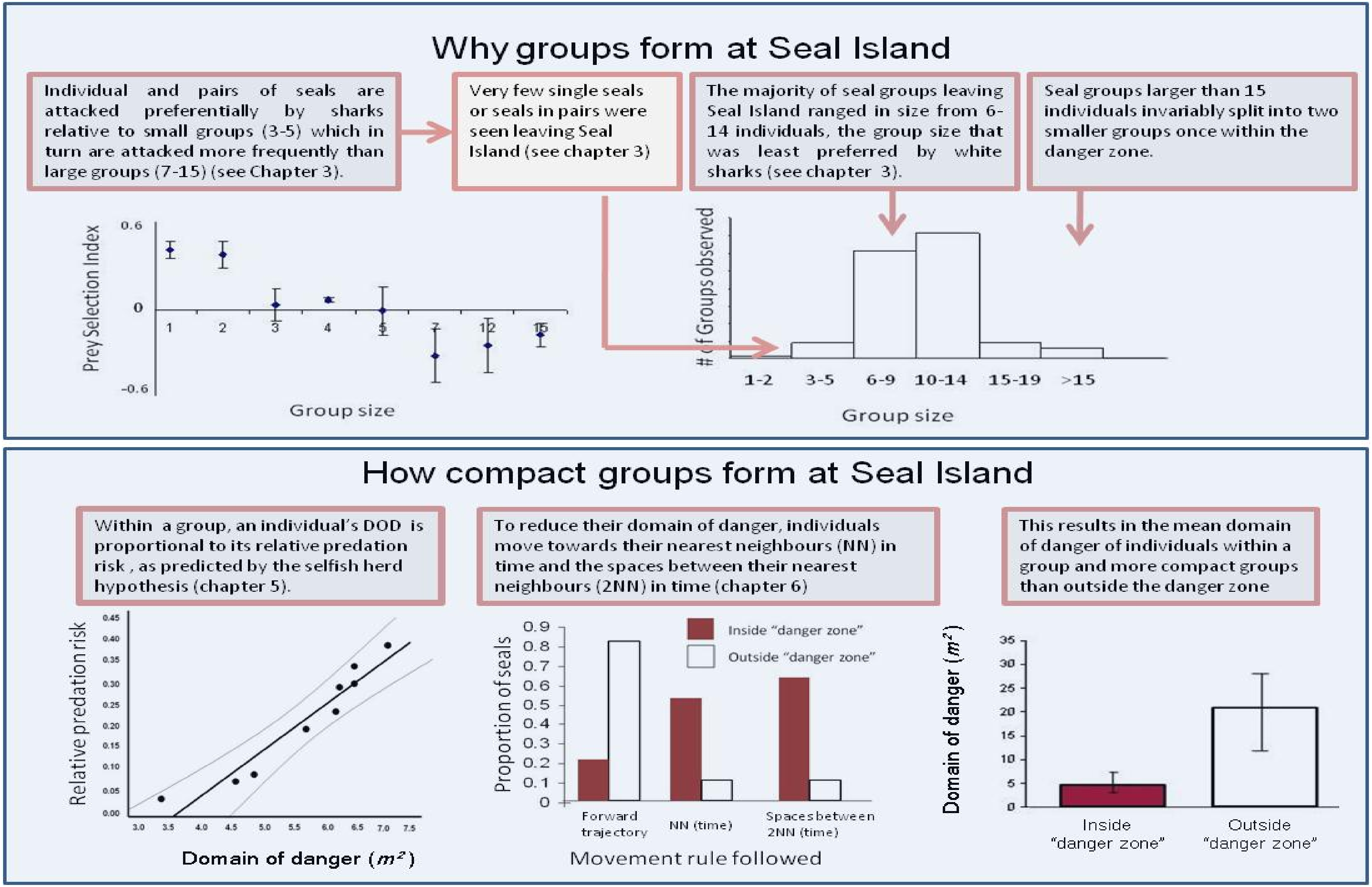
-This results in compact groups

At Seal Island

-To reduce individual domains of danger, individuals move towards their nearest neighbors in time and space.

-This results in a reduction of individual domains of danger and groups that are more compact

Figure 7.1.Schematic summary of how results in this study support the selfish herd hypothesis as an explanation for observed group size distribution in winter.



Why groups form at Seal Island

Individual and pairs of seals are attacked preferentially by sharks relative to small groups (3-5) which in turn are attacked more frequently than large groups (7-15) (see Chapter 3).

Very few single seals or seals in pairs were seen leaving Seal Island (see chapter 3)

The majority of seal groups leaving Seal Island ranged in size from 6-14 individuals, the group size that was least preferred by white sharks (see chapter 3).

Seal groups larger than 15 individuals invariably split into two smaller groups once within the danger zone.

How compact groups form at Seal Island

Within a group, an individual's DOD is proportional to its relative predation risk , as predicted by the selfish herd hypothesis (chapter 5).

To reduce their domain of danger, individuals move towards their nearest neighbours (NN) in time and the spaces between their nearest neighbours (2NN) in time (chapter 6)

This results in the mean domain of danger of individuals within a group and more compact groups than outside the danger zone

Figure 7.2. A schematic integration of the predictions and assumptions of the selfish herd with the broader framework within which grouping is understood (see chapter 1), and how results from this study at Seal Island support those predictions.

7.2.3. Emerging questions

White shark activity at Seal Island is highly seasonal and peaks during the austral winter when juvenile cape fur seals are making their first exploratory forays into deeper water (David *et al.* 1986). It thus seems highly plausible that the sharks congregate at the island to exploit an ephemeral, locally abundant prey source, namely naive juvenile seals. The greatly reduced white shark activity in late spring and early summer corroborates this suggestion as while prey remains locally abundant the young-of-the-year have learnt to avoid travelling alone in deep water during peak predation periods (i.e. the first three hours after sunrise). It would be ideal if shark hunting success could be quantified at the island to establish the cost/benefit relationship that almost certainly underpins the arrival and departure of sharks at Seal Island on annual basis. An alternative suggestion that would need to be quantified is that white sharks move away from the island because of the increased availability of alternative food sources, such as yellowtail and snoek, bony fish that proliferate in False Bay in spring and early summer (Lamberth *et al.* 1995). ,

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Factors influencing shark movement patterns in False Bay are not purely academic. White sharks provide a substantial amount of revenue to ecotourism ventures in False Bay. Tour operators attract sharks to their boats using both chum (minced fish food) and juvenile seal decoys. It is not known to what extent these activities attract white sharks to the Island and this remains an important area of research. The movement of sharks away from the island in early summer despite ongoing chumming and decoy use does however suggest only a minimal anthropogenic effect on shark attendance patterns at Seal Island. The increase in white shark activity in the inshore areas of False Bay in summer combined with increased recreational activities by humans (e.g. swimming, surfing and diving) has the undesired effect of increased spatial overlap between white sharks and humans in False Bay. This has resulted in 25 attacks in total between 1960 and 2005 (Cliff 2006), which is considered high internationally.

A second unanswered question is the absence of shark attacks at dusk. If the combination of limited light penetration (providing cover for sharks at depth) and backlit seal silhouettes swimming at the surface are the critical factors explaining the post-dawn peak in predation events then one would predict similar patterns at dusk when similar environmental conditions prevail. Shark attacks at another seal colony off the coast of South Africa follow a bimodal (dawn and dusk) pattern (Johnson *et al.* 2009), and thus the lack of dusk attacks remain an unexplained anomaly at Seal Island. Previous studies have noticed this pattern and have suggested that seal movement is depressed just before dusk (Laroche *et al.* 2008), but my results do not support this contention with no reduction in either adult or juvenile activity in the hours before sunset.

A third unanswered question is the role that sub-optimal predator behaviour plays in the system. I have considered sharks as a homogenous age class unit, but it may well be that sharks of different age, size and level of experience behave differently around the island (Johnson *et al.* 2009).

Lastly, this thesis focused on anti-predatory defences prior to attack (primary defences), but there is much scope to understand secondary defences. This aspect of seal biology has remained completely unstudied at Seal Island.

7.2.4. Implications for predator prey theory, shortfalls of the study, and concluding remarks

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My study demonstrates the usefulness of a novel biological system as a potential solution to long-standing theoretical challenges. In the test of the selfish herd hypothesis, for example, a major difficulty in testing the predictions has been the apparent artificiality of the original thought model (even Hamilton himself criticized this, Hamilton 1971). However, closer perusal of the literature show that whilst this hypothesis is often invoked to explain grouping behaviour in two-dimensional systems the original conditions under which it was developed approximated that of a 2-D, 3-D aquatic system, where animals on a 2-D plane are attacked by a predator in a 3-D plane. However, 2-D, 3-D aquatic systems are not often used to test the predictions of this hypothesis and Romey *et al.* (2008) even argue that these systems are inappropriate for testing the selfish herd hypothesis. They contest that if a predator comes approximately straight up or down the group, there would not be a large difference in proximity between targets and that all prey will consequently have similar domains of dangers. I argue that the prey’s domain of danger is, in fact, two-dimensional, as the selfish herd predicts that the predator takes the nearest individual to where it randomly appears “at the surface” (Hamilton 1971).

The risk allocation hypothesis fulfills the requirements of a testable hypothesis. Empirical studies of risk allocation hypothesis have provided equivocal results, largely as a result of artifacts within the experimental systems used. The advantage of this study was that descriptive data were used to inform the design of a quasi-experimental approach within a completely natural predator–prey system. Thus predation risk varied both on the short and long term temporal scale (daily and seasonally) in addition to spatially both within and between study sites. This heterogeneous landscape of predation risk allowed for the formulation of testable predictions based on the risk allocation hypothesis. It is nevertheless important to point out that it was not possible to derive an experimental and control study site as there a myriad of ecological factors, other than predation risk, which may influence the activity patterns of seals at a particular site. Egg Island was far from a perfect control site: in addition to the different in colony size, predation risk from other shark species was not quantified. Seven gill sharks are known to feed on cape fur seals throughout these seals’ range (Ebert 1991, 1996). Additionally, the (absence of) predation risk by white sharks at Egg Island should ideally be more thoroughly quantified in future studies.

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The importance of a quasi-experimental approach is similarly evident in the study on the selfish herd hypothesis (chapter 5) in which an artificial experiment was combined with the essential elements of a natural predator-prey system. Although arguably the most generally cited hypothesis in predator/prey systems the assumptions of the SHH are often only superficially addressed. In this study, I have been gone to great lengths to discuss the assumptions of the hypothesis and its suitability for explaining seal behavior at Seal Island. I conclude that the selfish herd is an empirically verified individual-based explanation for how individuals in loosely spaced groups may behave to maintain groups in compact units that serve to reduce predation risk to all individuals.

Perhaps the most obvious shortcoming within this thesis was that estimates of group compactness were not obtained at Seal Island during the low predation risk seasons (summer). While it was financial costs (i.e. helicopter flight) that constrained the collection of this data, this remains an important data set to obtain for further verification of the SHH. I showed that the mean group size of seals leaving the island was greater in summer (low predation risk) than winter (high predation risk). The SHH does not specifically address issues pertaining to group size and predation risk but it could nevertheless be argued that this result is somewhat confounding given that groups are thought to form in response to predation risk. If as I suggest groups form in winter and summer as a result of over-dispersion on a clumped resource then the key difference that will be predicted for groups in winter versus summer by the SHH is mean level of group compaction. I showed that group compaction was higher when seals in a given group were inside the high predation risk area around Seal Island. It remains to be shown that the same relationship holds for groups in the high versus low predation risk seasons.

In many ways the selfish herd hypothesis was ahead of its time. Currently biologists are calling for a unification of mechanistic and evolutionary biology (Sumpter 2006), an objective that the predictions of Hamilton’s hypothesis have been achieving for more than 38 years. The major challenge for future work on this hypothesis will be to further integrate it into the relatively recently emerged fields of self-organization (Couzin *et al.* 2003, Sumpter 2006) and consensus decision making (Conradt and Roper 2003, 2005, 2009).

Grouping under predation risk is one of the most widely researched topics in biology, with numerous theoretical and mathematical models in existence to explain how animals should behave in groups and even more empirical studies which attempt to describe how animals do behave in groups. In this thesis, my aim was simply to show the value of integrating these approaches.

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"Yet although the ox has so little affection for, or individual interest in, his fellows, he cannot endure even a momentary severance from his herd. If he be separated from it by stratagem or force, he exhibits every sign of mental agony; he strives with all his might to get back again and when he succeeds, he plunges into its middle, to bathe his whole body with the comfort of closest companionship."

-*Francis Galton, 1871* on observing cattle in the North of what was then German South West Africa

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Table and Figure legends

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Tables

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