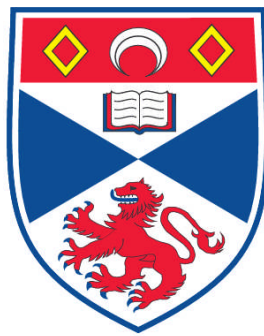


**THE TRADE-OFF BETWEEN STARVATION AND PREDATION
RISK IN OVERWINTERING REDSHANKS (TRINGA TOTANUS)**

Alex Sansom

**A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews**



2010

**Full metadata for this item is available in the St Andrews
Digital Research Repository
at:**

<https://research-repository.st-andrews.ac.uk/>

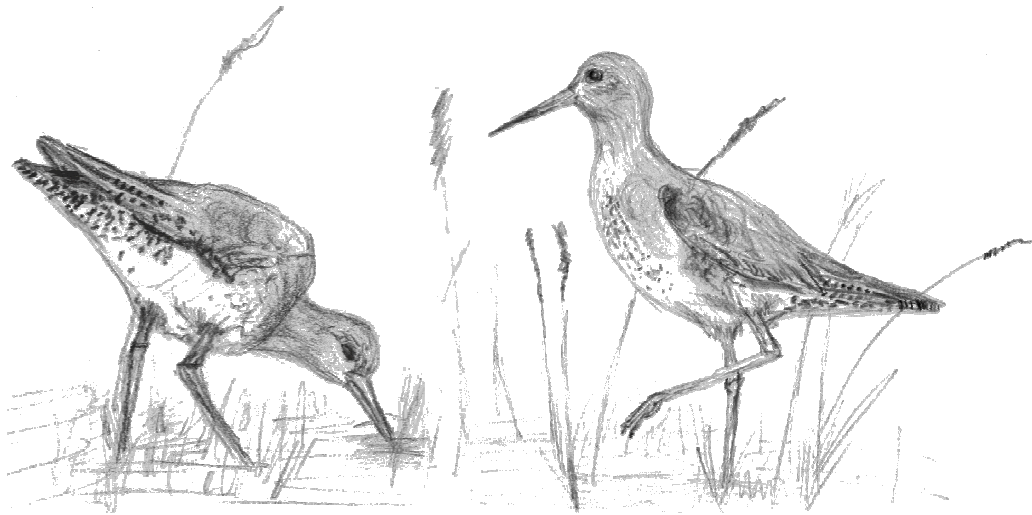
Please use this identifier to cite or link to this item:

<http://hdl.handle.net/10023/890>

This item is protected by original copyright

**This item is licensed under a
Creative Commons License**

The Trade-off Between Starvation and Predation Risk in Overwintering Redshanks (*Tringa totanus*)



Alex Sansom

Submitted for the degree of Doctor of Philosophy to the University of
St-Andrews

August 2009

Supervisor: Dr. Will Cresswell

ABSTRACT

In order to meet their energy budget animals must often increase their risk of predation, either through their choice of foraging location or by decreasing anti-predation behaviours, which are incompatible with foraging. I investigated the starvation-predation risk trade-off in redshanks overwintering in the area of the Firth of Forth in Scotland over different spatial scales. On a small spatial scale, where redshanks foraged in an area where risk of attack was high I investigated the role of competition for food and decreased individual vigilance within groups and how this related to predation risk, additionally I looked at the relative roles of individual variation in time spent exposed to risk and variation in anti-predation behaviours on individual survival time. On larger spatial scales of 100s of meters and over several kilometres, I considered how choice of overwintering site was affected by predation risk, profitability and population density. Time available to feed increased with increased group size, allowing redshanks to compensate for increased competition and allowing large groups to form, thus decreasing individual predation risk. Individuals that spent less time exposed to attacking predators survived for longer, however individuals constrained by cold weather to spend long periods exposed to risk could increase their survival through increased intake rates and vigilance. On an intermediate spatial scale redshanks selected overwintering sites based on profitability rather than risk, and only used less profitable site when population density was high. On a large spatial scale increased their use of less profitable sites in warmer weather, but did this without increasing their risk of predation. Overall this suggests that across most spatial scales redshanks can minimise their predation risk by their choice of foraging location, but when forced by weather conditions or competition to be exposed to attack, capture reducing behaviours also reduce predation risk.

I, Alex Sansom hereby certify that this thesis, which is approximately 30000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in September 2005 and as a candidate for the degree of Doctor of Philosophy in September 2005; the higher study for which this is a record was carried out in the University of St Andrews between 2005 and 2009.

date 17/12/09 signature of candidate

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

date 17/12/09 signature of supervisor

In submitting this thesis to the University of St Andrews we understand that we are giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. We also understand that the title and the abstract will be published, and that a copy of the work may be made and supplied to any bona fide library or research worker, that my thesis will be electronically accessible for personal or research use unless exempt by award of an embargo as requested below, and that the library has the right to migrate my thesis into new electronic forms as required to ensure continued access to the thesis. We have obtained any third-party copyright permissions that may be required in order to allow such access and migration, or have requested the appropriate embargo below.

The following is an agreed request by candidate and supervisor regarding the electronic publication of this thesis:

Access to Printed copy and electronic publication of thesis through the University of St Andrews.

date 17/12/09 signature of candidate signature of supervisor

ACKNOWLEDGEMENTS

A great many people have helped me get through my PhD by supporting me in various ways, but none more so than my supervisor Will Cresswell, by providing advice, encouragement, and even by being a field assistant; basically by always helping in exactly the way I needed. He has made my PhD an extremely positive experience.

Without the help of all the people who helped catching redshanks at Tynninghame I couldn't have collected any individual behavioural data, so thanks to all those who endured the cold and sometimes wet weather to chase redshanks around the saltmarsh. I also am very grateful to Johan Lind for collecting so many behavioural videos at Tynninghame, providing input and advice on the behaviour and survival chapter, and for being much needed and very good company during the first winter of my PhD. Many thanks to Mark Rehfisch, Niall Burton and Graham Austin for the time they spent discussing the analysis of the WeBS data and all the advice and ideas I gained from my meetings with them. I also thank the BTO for supplying me with the WeBS data used in chapter 5, and all those involved in providing this data and the GIS information for the count sectors; of course many thanks to all the volunteers who, over the years, collected the WeBS data on which this chapter was based. Thanks to the British Atmospheric Data Centre for providing the weather data for chapter 5 and making data freely available to PhD students. Monique Mackenzie from CREEM provided me with some invaluable statistical advice on analysing the WeBS data and I should also thank Theoni Photopoulos for taking the time to discuss and advise on using Generalised estimating equations.

I must also thank all the friends I have made in St-Andrews, for making it such a fantastic place to live and study; especially to Amy, Valentina, Emma, Katie and Tess who have always been there to listen, or just to supply chocolate and red wine. Finally I am very grateful to my family for always encouraging and supporting me in what I choose to do even if they don't understand why and to Mark who has had to put up with me over the last few months, and who is always there for me even when I am being a horrible person.

My research was funded by a NERC quota studentship awarded to the University of St-Andrews.

Table of Contents	Page Number
CHAPTER 1: Introduction	1
THE ROLE OF PREDATION RISK	1
REDUCING PREDATION RISK	2
The avoidance-capture continuum	6
Spatial and temporal scales and the avoidance-capture continuum	7
MEASURING THE EFFECTS OF PREDATION RISK	8
THE FORAGING COST OF PREDATION	9
SYNTHESIS: AN INTEGRATED APPROACH TO DETERMINING THE IMPORTANCE OF PREDATION RISK	11
THESIS OVERVIEW	11
REFERENCES	13
 CHAPTER 2:	
Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit?	22
ABSTRACT	23
INTRODUCTION	24
METHODS	25
Study Site	25
Ringing	26
Focal Observations	26
Analysis	27
RESULTS	28
DISCUSSION	36
ACKNOWLEDGMENTS	38
REFERENCES	38
 CHAPTER 3:	
Individual behaviour and survival: the roles of predator avoidance, foraging success and vigilance.	42
ABSTRACT	43
INTRODUCTION	44
METHODS	47
Study Site	47
Ringing	47
Focal Observations	47
Measuring behaviour	49
Estimating time spent on the saltmarsh	49
Measuring survival	50
RESULTS	52
Model 1: individual survival is primarily determined by avoidance of risky areas	52
Model 2: individual survival in high-risk areas is determined by foraging and vigilance	52
DISCUSSION	56
ACKNOWLEDGEMENTS	58
REFERENCES	59

CHAPTER 4:**How is the distribution of redshanks (*Tringa totanus*) overwintering on the Fife coast related to habitat profitability, predation risk, starvation risk and population density?**

	65
ABSTRACT	66
INTRODUCTION	67
METHODS	70
Study system	70
Measuring site use by redshanks	71
Index of predation risk	71
Habitats and profitability	71
Measuring sector characteristics	72
Weather data	73
Model Parameters	73
Analysis	74
RESULTS	75
Effects of temperature on distribution between sectors	75
Effects of temperature on distribution within sectors	76
Population density effects on distribution	76
DISCUSSION	79
REFERENCES	83

CHAPTER 5:**The distribution of overwintering redshanks (*Tringa totanus*) in the Firth of Forth over 12 years with respect to profitability and predation risk: Is there any evidence for a starvation-predation risk trade-off?**

	89
ABSTRACT	90
INTRODUCTION	91
METHODS	94
Study system	94
Site use by redshank in the Firth of Forth	94
Index of predation risk	95
Index of profitability	95
Measuring sector Characteristics	96
Weather data	96
Model Parameters	97
Analysis	97
RESULTS	99
Comparison of high and low tide distributions	99
Yearly temperature effects on redshank distribution	100
Investigation of monthly measures of temperature on redshank distribution	101
Frost days in a month	101
Matched minimum temperature	106
DISCUSSION	111
REFERENCES	114

CHAPTER 6: Discussion**Redshanks as a case study of the predation-starvation risk trade-off**

	121
AVOIDING ATTACK: BEHAVIOUR WHEN EXPOSED TO ATTACK	124

CHOICE OF FORAGING LOCATION	125
OTHER FACTORS AFFECTING STARVATION AND PREDATION RISK	127
The role of predator behaviour	127
The roles of environmental conditions and population density	127
REDSHANK SYNTHESIS AND AREAS FOR FURTHER RESEARCH	128
GENERAL SYNTHESIS	130
REFERENCES	132
APPENDIX 1	139

CHAPTER 1: INTRODUCTION

THE ROLE OF PREDATION RISK

During an animal's lifetime it is reasonable to assume that any individual that can decrease its probability of being caught by a predator will have increased fitness, through longer survival time and the increased opportunities for reproduction that this will afford. Given that failure to avoid predation carries such a high cost to fitness it is no surprise that over evolutionary time predation has been linked to key physical and behavioural adaptations such as cryptic colouration, startle responses and physical and behavioural adaptations that aid flight from an attacking predator (see Endler 1991; Lima and Dill 1990 and Lima 1998b).

Depredation of prey animals, risk of predation and the behavioural decisions that animals make when trying to reduce their risk of predation act not only at the individual level but also have an impact on populations (Lima and Zollner 1996; Biro *et al.* 2003 and Goss-Custard 1996). Risk of predation can determine both where and when animals choose to feed, reproduce and migrate (for example Elchuk and Wiebe 2002; Roos and Pärt 2004; Schmaljohann and Dierschke 2005; Alerstam and Lindstrom 1990). Risk of predation is often a strong influence on decisions related to living or foraging in groups (Krause and Ruxton 2002; Bednekoff and Lima 1998 and Elgar 1989) which then affects the way in which individuals within populations interact and compete for resources (Beauchamp 1998; Bednekoff and Lima 2004). The impact of predation risk in determining where animals choose to spend time also creates competition for the 'safest' position, whether this is a nest site, a foraging area or a position within a group (Hamilton 1971; Petit and Bildstein 1987; Grand 2002; and Nilsson 1984). This type of competition often leads to populations being structured in space and/or time by age, sex, condition, or dominance (Cresswell 1994; Grubb and Woodrey 1990; and Lahti 1998). Predation of specific classes of individuals can also determine the age structure or sex ratio within a population (Koivunen *et al.* 1996).

Due to the effects that predation risk has on the day-to-day decisions animals make, its impact also extends to the structuring of whole ecosystems. Interactions between predators and prey or the response of prey to perceived risk can impact on prey and

predators directly and indirectly, and affect other species outside the predator species-prey species interaction (Werner and Peacor 2003; Wooster and Sih 1995). Predation pressure on one prey species can directly alter its abundance and behaviour and may also indirectly alter the abundance of a competitor for a common resource (Peacor and Werner 2001). Changes in the density of a preferred prey type can cause predators to alter their diet, directly affecting mortality in alternative prey species (Dunn 1977; Marcstrom *et al.* 1988). Ecosystem effects can also occur as a result of ‘non-lethal’ effects of predators (Lima 1998a and Cresswell 2008). For example where perceived predation risk causes shifts in populations of herbivores or changes in herbivore activity, this then also impacts on vegetation within an ecosystem (Schmitz *et al.* 1997). Given that ‘non-lethal’ effects of predation risk may cause a population of one prey type to move to a safer area, this can result in predators also changing their hunting strategy either by moving, or possibly by targeting an alternative prey species (Lima 2002; Lima *et al.* 2003).

REDUCING PREDATION RISK

Bearing in mind the cost to fitness, animals should reduce predation risk whenever possible. Reducing the probability of being depredated consists of reducing probability of being attacked, and if attacked, reducing probability of being caught (see Lima and Dill 1990):

*Probability of death from Predation=Probability of attack*Probability of capture when attacked.*

Prey animals can use a wide range of anti-predation behaviours, strategies or adaptations to modify one or both of these probabilities to increase their probability of survival (for example references see Table 1.1). The point at which risk is reduced will be dependant on a prey species’ ecology and particularly the ecology and range of their predators. A crucial aspect of this will be the spatial and temporal scale over which the predator and prey operate. If prey can avoid predators in time and/or space then selection will act to promote avoidance traits. If prey cannot avoid predators then selection will act to promote capture-reducing traits (Lima and Dill 1990; Lima 1992). Some traits, however, act to reduce avoidance and/or capture, dependent on ecological circumstances and predator behaviour. There is therefore a continuum of anti-

predation traits operating from mainly avoidance promoting traits to mainly capture reducing traits (Figure 1.1). This continuum approach is important because it explicitly recognises the importance of variation in the probability of predator and prey encountering each other on selection for different traits. The continuum approach also allows a clear appreciation of the dynamic nature of predator-prey interactions. For example, an effective capture reducing trait may lead to a reduced predator attack rate because the predator then concentrates on easier to capture prey. Similarly, selection for avoidance behaviours will reduce selection for capture reducing behaviours and vice-versa (Brodie and Formanowicz 1991).

Figure 1.1. (See over leaf) Illustration of the attack-avoidance continuum, showing examples of ways in which animals can reduce their risk of predation by reducing their probability of capture and/or probability of attack. The way in which attack reducing and avoidance behaviours interact and feedback to predator hunting decisions is also illustrated. As exposure to or spatial and temporal overlap with predators increases, so selection ‘switches’ from avoidance to attack reducing traits. Most animals occupy the ‘grey’ middle area where neither perfect avoidance nor perfect defences are achieved and where selection on attack reducing and predator avoidance traits varies with spatial and temporal variation in exposure to attacking predators.

Probability of death from predation =

Probability of Attack

1.) Forage completely away from Predators

- a. Avoidance in space
- b. Avoidance in time

2.) Forage under risk of predator occurrence but reduce risk of attack using:

- a. Cover/refuges
- b. Crypsis, reduced activity
- c. Solitary foraging
- d. Availability of alternative prey
- e. Warning colouration
- f. Early detection of predator presence

Increased attack probability leading to stronger selection on capture reducing traits



Effective capture reducing behaviours, leading to reduced attack rate as predators target alternative prey.

Probability of Capture

3.) Forage under risk of predator occurrence but reduce risk of being targeted during attack:

Foraging in a group:

- i. Increased chance of early detection of an attacking predator.
- ii. dilution of predation risk
- iii. confusion effect
- iv. selfish herd

4.) Forage under risk of predator occurrence but reduce risk of capture during attack:

- a. Escape behaviours and appropriate responses
- b. Pursuit deterrence

5.) Forage invulnerably with predators

- a. Size
- b. Poisons
- c. Armour

Continuum of selection shifting from avoidance traits to capture affecting traits

overlap of predators with prey

Table 1.1. Examples of the variety of different behaviours and adaptations which animals use to avoid or reduce predation risk, and the point at which risk of predation is reduced. Examples of complete avoidance or complete invulnerability are not included.

Point at which risk is reduced	Species	Evidence of Risk reducing strategy	Reference
Before attack	Salamander larvae (<i>Ambystoma barbouri</i>)	Avoid pools containing fish predators	(Sih <i>et al.</i> 1992)
	Rats	Shift from nocturnal to diurnal activity in response to fox activity	(Fenn and Macdonald 1995)
	Snails	Refuges are used more when closer to a predatory fish	(Turner and Montgomery 2003)
	Ghost swift moths	Use ‘acoustic crypsis’ (Fly close to vegetation) when under risk of predation from bats	(Rydell 1998)
	Coho salmon	Reduce activity in the presence of a predatory duck	(Martel and Dill 1995)
	Monkeys	Predation by leopards is greater when groups are larger, possibly due to detection effects	(Zuberbühler and Jenny 2002)
	willow tits and crested tits	Only forage in risky locations on trees in years when high densities of voles mean that predation risk from owls is low	(Suhonen 1993)
During attack (before targeted)	Wood pigeon	Early detection of a predator increases chance of survival	(Kenward 1978)
	Thomson’s gazelle	Predators less likely to target vigilant individuals	(Fitzgibbon 1989)
	Red-Necked pademelon	Whilst foraging, increased risk of predation is compensated for by changes in vigilance, group size, and distance to cover.	(Wahungu <i>et al.</i> 2001)
	Butterflies	Decreased predation risk with increased group size (dilution effect).	(Burger and Gochfeld 2001)

	Crabs	Individuals in groups move closer together when attacked by a predator	(Viscido and Wethey 2002)
During attack (once prey is targeted)	Ungulates	Pursuit deterrence signalling (e.g. tail flagging) used	(Caro <i>et al.</i> 2004)
	Common lizards	Escape performance affects chance of being captured by a predator	(Clobert <i>et al.</i> 2000)
During attack or before attack (can affect attack success or chance of being attacked)	Fish	Predatory pike are limited in the size of prey they can feed on larger individuals are less vulnerable, increasing selection on fast growth rates	(Nilsson and Christensen 2000)
	Neotropical poison frogs	Forage on small alkaloid containing arthropods to sequester defensive alkaloids in their skin	(Darst <i>et al.</i> 2005)
	Marine gastropods	When exposed to chemical cues from predators or damaged conspecifics shells are more predator resistant	(Appleton and Palmer 1983)

The avoidance-capture continuum

Perfect avoidance or perfect defences against capture eliminate predation risk because they make the probability of being attacked or that of being captured zero (Lima 1998a; Mao *et al.* 2005; Valeix *et al.* 2009). This is the ‘ideal’ situation and as such there should be strong selective pressure on individuals to feed away from predators whenever possible or to develop mechanisms by which any attack will not result in capture or death. Except in a few circumstances, such as predator free islands (Blumstein and Daniel 2005), most animals do not achieve this all or even some of the time and use ‘intermediate’ strategies to reduce risk of depredation. The extent to which animals become specialised to cope with predation risk will be dependant on how constrained they are to being exposed to attacking predators (Lima and Bednekoff 1999). Animals that are highly mobile, meaning that they can respond to risk in a flexible and varied way are likely to have less-specific anti-predation strategies compared to non-mobile individuals that cannot avoid constant exposure to attack. Highly mobile individuals can alter their foraging location or move to forage with other individuals, whereas individuals that cannot move in response to risk must

adapt defences to reduce their risk of being captured or eaten when attacked in other ways (Brodie and Formanowicz 1991). An important point to make is that spatial and temporal avoidance function in a similar way in terms of selection. The ‘further’ from the point of attack an animal is in both space and time the stronger the selection will be on behaviours that enable this separation and promote survival through avoidance; the closer in time or space to the point of attack, the more specific the response or adaptation will be to reduce risk of capture.

When considering the range of strategies used to reduce predation risk it is clear that some behavioural ‘options’ can reduce both risk of attack and capture (Figure 1.1). This makes it unclear to what extent behaviours such as choice of foraging location are ‘attack reducing’ or ‘capture reducing’ and blurs the boundary between these categories. For example if an individual forages far from predator concealing cover then it reduces its risk of capture when attacked (Whitfield 2003; Pomeroy *et al.* 2006); however, given that an attack is less likely to be successful, a predator may choose to avoid targeting this individual thus the behaviour also reduces the risk of attack (Quinn and Cresswell 2004). It is therefore important to consider the feedback effect that the decisions and adaptation of prey have on predator hunting decisions (Lima 2002). Similarly an animal that is invulnerable to capture because of armour or its use of a refuge, will never be attacked. Animals that appear in the bottom part of the conceptual diagram in Figure 1.1 because of their effective capture reducing traits could therefore be considered also at the top of the diagram, where perfect attack avoidance has been achieved.

Spatial and temporal scales and the avoidance-capture continuum

Traits, which act to reduce risk at more than one point along the avoidance-capture continuum, can be best understood when spatial and temporal scales are taken into account. As spatial scale decreases, the point at which risk is reduced is likely to be closer to the point to attack: in other words selection shifts from avoidance to capture reducing behaviours as spatial scale decrease. For example on large spatial scales individuals can avoid predators completely by moving away from areas that pose a higher predation risk (Lima 1998a; Werner and Peacor 2003). Individuals can also make adjustments on a smaller spatial scale to their foraging location, for example foraging closer to a conspecific, which will reduce risk of capture when attacked

(Hamilton 1971). When considering temporal scale the same behaviour can act to reduce risk before or during an attack, for example vigilance can increase detection of a non-attacking predator enabling action to be taken to avoid attack, or once a predator is attacking, early detection can result in rapid escape responses and decrease risk of capture (Lind 2004).

Clearly, understanding the role of behaviour over different spatial and temporal scales is important in understanding the strength of selection operating on avoidance and capture reducing behaviours. Also considering a strategy over long and short time scales can give insights into evolution of predator-prey interactions. This is best summarised by a classic example. The emergence of large numbers of periodic cicadas at the same time will dilute each individual's risk of depredation and so can be considered as a capture reducing behaviour. However, when considered as a long-term strategy the long time periods between emergence, and the fact that the length of these periods are prime numbers mean that predators cannot adapt for specialising on cicadas, thus avoiding a predator-prey arms race. This approach adopted in this thesis incorporates these ideas: how spatial and temporal scale results in differing strengths of selection on avoidance and capture reducing behaviours.

MEASURING THE EFFECTS OF PREDATION RISK

The most direct cost of predation is death; therefore a good way to measure the effect of predation on fitness is to look at individual or population death rates or survival times. If variation in anti-predation behaviours can be linked to variation in survival or death then this gives us a clear association between ability to reduce risk and fitness (Lind and Cresswell 2005). There are many examples where this approach is relevant and has been successfully used. For example increased levels of activity in the presence of a predator have often been linked to increased death rates (Anholt and Werner 1995; Anholt and Werner 1998; Downes 2002), and the benefits of living in groups have also often been directly linked to survival (Kenward 1978; Uetz *et al.* 2002; Watson *et al.* 2007).

However studies that link death rates to behaviours often focus on capture reducing behaviours or just the effects of removal of individuals from a system, rather than avoidance, the interaction between avoidance and capture or the way in which

reducing predation risk interacts with other aspects of fitness (Lind and Cresswell 2005; Lima 1998a and Lima and Zollner 1996). This means that sometimes measuring death rates may be misleading, or too simplistic, because perfect avoidance of attack or capture by predators has no survival implications but could lead to big fitness decrements. Animals can often decrease their risk of predation, but at a cost to another aspect of their fitness, for example allocation of resources to predator avoidance in wolf spiders *Pardosa milvina* leads to the production of fewer eggs (Persons *et al.* 2002). Therefore it is important to consider the costs and benefits of reducing predation risk when studying its effects. One productive approach to this is to consider the trade-off between risk of predation and risk of starvation (Brown and Kotler 2004).

THE FORAGING COST OF PREDATION

As mentioned animals must avoid predation if they are to survive and breed; however individuals also need to feed to avoid starvation. Foraging is often incompatible with avoiding detection and/or capture by predators, for example even just an increase in activity associated with searching for food can increase detection by predators (for example Biro *et al.* 2003; Biro *et al.* 2004; Downes 2002; Anholt and Werner 1995; Sih 1986). Therefore one of the major trade-offs animals make that will affect fitness is between feeding activity and minimising predation risk (Brown and Kotler 2004 and Lima and Dill 1990). This feeding-risk avoidance trade-off means animals often 'lose-out' on foraging gains at the expense of avoiding or reducing predation risk. Reduced food intake rates resulting from lowered foraging activity in the presence of predators can affect growth rates and the time taken to reach maturity (Westerberg *et al.* 2004). This may delay reproduction and could also affect fitness directly (in terms of survival) if smaller body size or slow development is associated with vulnerability to predators (Bosque and Bosque 1995; Hoare *et al.* 2000). Other behaviours, which are incompatible with foraging can also reduce food intake, for example anti-predator vigilance is often incompatible with searching for prey so that more vigilant individuals may also have lower food intake rates (Beauchamp 2005; Illius and Fitzgibbon 1994). The same effects can occur when animals forage in groups where there is competition for food; individual risk is reduced as groups size increases through dilution, increased detection or confusion of predators (Krause and Ruxton

2002) but individual intake rates may also be lower (Beauchamp 1998; Bachman 1993).

Animals may also effectively be excluded from the most profitable foraging areas by risk of attack. It is often the case that animals will choose to forage in areas that pose a lower risk of predation even if they do not provide the most profitable foraging environment (Abramsky *et al.* 1996; Lindstrom 1990; McLoughlin *et al.* 2005). In reducing its predation risk an animal may survive, but investment in anti-predation behaviours that are incompatible with foraging or avoiding risky but profitable feeding areas may have other fitness-reducing effects, such as poor body condition, lower competitive ability or reduced breeding success. For example, foraging gains and body condition may affect the quality or number of offspring produced (Ball and Baker 1996; Persons *et al.* 2002).

When foraging gains are sufficiently high, or when animals are under energetic stress, individuals may make foraging decisions that increase their intake rate but at a cost to increasing their predation risk (Kotler and Blaustein 1995; Brown and Kotler 2004). For example animals may choose to feed away from a group where risk would be lower to avoid competition and maximise their food intake (Hensor *et al.* 2003) or, when energetically stressed, individuals may forage in an area which is rich in food but also poses a greater risk of predation (Pettersson and Bronmark 1993; Pomeroy *et al.* 2008). This trade-off, of course, means that individuals can be constrained to forage under risk of attack for reasons other than lack of mobility. Competition, increased energy budget or energetic stress, lack of suitable habitat or food resources can all force individuals to forage in areas or situations where they will be exposed to predators and must reduce their predation risk by reducing risk of attack and risk of capture. Temporal variation in these factors, which constrain animals to forage under risk of predation, will result in variation in the extent to which individuals rely on avoidance compared to mitigation against risk of attack and capture and will lead to variable selection pressure on different anti-predation behaviours over time (Lima and Bednekoff 1999).

SYNTHESIS: AN INTEGRATED APPROACH TO DETERMINING THE IMPORTANCE OF PREDATION RISK

Selection for particular traits to reduce predation risk depends on the temporal and spatial scale over which predator and prey can potentially interact. The strength of any selection needs to be measured in terms of overall survival probabilities and foraging costs of anti-predation behaviours. Knowledge of the costs of avoiding risk, for example, that animals are often trading off food for safety or vice versa, and how exposure to risk and selection on risk reducing behaviours fluctuate in space and time, can therefore give us real insights into why animals behave in the way that they do and how individual behavioural decisions lead to survival, reproductive output, population dynamics and community structure.

When examining selection for anti-predation behaviours it is also important to remember that animals can use multiple behaviours to balance predation risk with starvation risk and that these behaviours can interact (Lind and Cresswell 2005). Altering one aspect of behaviour that decreases starvation risk at a cost to increased predation risk can be compensated for by another aspect of behaviour, or animals can use a whole suite of behaviours to reduce risk whilst foraging under risk of predation (for example Williams *et al.* 2003; Sih *et al.* 2003; Kotler *et al.* 2004). Of course, predators are not passive in this process, changing their own response in real time to those of their prey, so feeding back to prey responses, eliciting further alterations in anti-predation behaviour (Lima 2002). The fact that animals use of multiple behaviours to respond to predation risk, and can use alternative behavioural strategies to cope with risk, as well as the fact the risk and the trade-off between foraging and predator avoidance varies in space and time means that one of the most effective ways to assess the effects of predation risk is to study behaviour in context using field systems. Considering selection on anti-predation behaviour using a field approach means multiple spatial scales can be considered in a natural system where animals are free to use multiple aspects of behaviour to manage the foraging costs of predation risk.

THESIS OVERVIEW

In this thesis I investigate the effects of predation risk on the behaviour and distribution of redshanks (*Tringa totanus*) overwintering on the east coast of Scotland

in area of the Firth of Forth. I study the trade-off between predation risk and starvation risk using field-data collected at different spatial scales to address the following questions:

1. What are the foraging costs and reduced predation risk benefits from feeding in a group? I investigate the relative effects of reduced individual vigilance and competition on individual intake rates in order to ascertain if redshanks feeding in flocks gain a foraging advantage in addition to reduced predation risk. Alternatively, increased competition may incur a cost to foraging in a flock so limiting the anti-predation benefits of vigilance accrued from the group size effect.
2. How does individual variation in anti-predation behaviour relate to survival? I compare the relative effects of predator avoidance and behaviours, such as vigilance, that reduce the risk of capture, on individual survival. I also consider the effect variation in environment conditions, which affect starvation risk, has on the extent to which individuals are exposed to risk and the role this plays in maintaining selection on avoidance and capture-reducing anti-predation behaviours.
3. How do starvation risk and predation risk affect the distribution of overwintering redshanks? In the final two chapters I consider the trade-off between starvation risk and predation risk on larger spatial scales. I investigate how risk of starvation and predation affect habitat choice of overwintering redshanks over two spatial and temporal scales:
 - a. Over one winter I consider how redshanks are distributed according to the food and predation risk attributes of areas along a section of coastline. I investigate how increased starvation risk, caused by cold weather, or increased competition, caused by higher population density, causes redshanks to trade-off food for safety, and results in changes in distribution over a scale of 100s of meters, through a winter.
 - b. Over 12 winters I consider the distribution of redshanks with respect to profitability and predation risk across the Firth of Forth. Again I consider if variation in starvation risk, due to cold weather, causes

redshanks to trade-off food for safety and results in changes in distribution over a scale of kilometres. Within this I consider variation in starvation risk at three temporal levels variation between years, between months and within a few days of when surveys were conducted.

REFERENCES

Abramsky, Z., Strauss, E., Kotler, B. P., Riggs, G., and Riechman, A. (1996). The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G.pyramidum*. *Oecologia* **105**, 313-319.

Alerstam, T. and Lindstrom, A. (1990). Optimal bird migration: the relative importance of time, energy and safety. In 'Bird Migration: physiology and ecophysiology.' (Ed E. Gwinner.) pp. 331-351. (Springer-Verlag: Berlin.)

Anholt, B. R. and Werner, E. E. (1995). Interaction between food availability and predation mortality mediated by adaptive behaviour. *Ecology* **76**, 2230-2234.

Anholt, B. R. and Werner, E. E. (1998). Predictable changes in predation mortality as a consequence of changes in food availability and predation risk. *Evolutionary Ecology* **12**, 729-738.

Appleton, R. D. and Palmer, A. R. (1983). Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in marine gastropod. *Proceeding of the National Academy of Sciences of the United States of America* **85**, 4387-4391.

Bachman, G. (1993). The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. *Animal Behaviour* **46**, 233-244.

Ball, S. L. and Baker, R. L. (1996). Predator-induced life history changes: Antipredator behavior costs or facultative life history shifts? *Ecology* **77**, 1116-1124.

Beauchamp, G. (1998). The effect of group size on mean food intake rate in birds. *Biological Reviews of the Cambridge Philosophical Society* **73**, 449-472.

- Beauchamp, G. (2005). Low foraging success of semipalmated sandpipers at the edges of groups. *Ethology* **111**, 785-798.
- Bednekoff, P. A. and Lima, S. L. (1998). Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proceedings of the Royal Society of London Series B* **265**, 2021-2026.
- Bednekoff, P. A. and Lima, S. L. (2004). Risk allocation and competition in foraging groups: reversed effects of competition if group size varies under risk of predation. *Proceedings of the Royal Society of London Series B* **271**, 1491-1496.
- Biro, P. A., Abrahams, M. V., Post, J. R., and Parkinson, E. A. (2004). Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society of London Series B* **271**, 2233-2237.
- Biro, P. A., Post, J. R., and Parkinson, E. A. (2003). From individuals to populations: prey fish risk-taking mediates mortality in whole system experiments. *Ecology* **84**, 2419-2431.
- Blumstein, D. T. and Daniel, J. C. (2005). The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B-Biological Sciences* **272**, 1663-1668.
- Bosque, C. and Bosque, M. T. (1995). Nest predation as a selective factor in the evolution of development rates in altricial birds. *American Naturalist* **145**, 234-260.
- Brodie, E. D. and Formanowicz, D. R. (1991). Predator avoidance and antipredator mechanisms - distinct pathways to survival. *Ethology Ecology & Evolution* **3**, 73-77.
- Brown, J. S. and Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters* **7**, 999-1014.

Burger, J. and Gochfeld, M. (2001). Smooth-billed ani (*Crotophaga ani*) predation on butterflies in Mato Grosso, Brazil: risk decreases with increased group size. *Behavioural Ecology and Sociobiology* **49**, 482-492.

Caro, T. M., Graham, C. M., Stoner, C. J., and Vargas, J. K. (2004). Adaptive significance of antipredator behaviour in artiodactyls. *Animal Behaviour* **67**, 205-228.

Clobert, J., Oppliger, A., Sorci, G., Ernande, B., Swallow, J. G., and Garland, T. Jr. (2000). Trade-offs in phenotypic traits: endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*. *Behavioural Ecology and Sociobiology* **27**, 153-157.

Cresswell, W. (1994). Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *Journal of Animal Ecology* **63**, 589-600.

Cresswell, W. (2008). Non-lethal effects of predation in birds. *Ibis* **150**, 3-17.

Darst, C. R., Menendez-Guerrero, P. A., Coloma, L. A., and Cannatella, D. C. (2005). Evolution of Dietary Specialization and Chemical Defense in Poison Frogs (Dendrobatidae): A Comparative Analysis. *American Naturalist* **165**, 56-69.

Downes, S. J. (2002). Does responsiveness to predator scent affect lizard survivorship? *Behavioural Ecology and Sociobiology* **52**, 38.

Dunn, E. (1977). Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. *Journal of Animal Ecology* **46**, 633-652.

Elchuk, C. L. and Wiebe, K. L. (2002). Food and predation risk as factors related to foraging locations of Northern Flickers. *Wilson Bulletin* **114**, 349-357.

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the evidence. *Biological Review* **64**, 13-33.

Endler, J. A. (1991). Interactions between predators and prey. In 'Behavioural Ecology: An Evolutionary Approach.' (Eds J. R. Krebs and N. B. Davies.) pp. 169-196. (Blackwell: Oxford.)

Fenn, M. G. P. and Macdonald, D. W. (1995). Use of middens by red foxes: Risk reverses rhythms of rats. *Journal of Mammalogy* **76**, 130-136.

Fitzgibbon, C. D. (1989). A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Animal Behaviour* **37**, 508-510.

Goss-Custard, J. D. (1996). 'The Oystercatcher: from individuals to populations.' (Oxford University Press: Oxford.)

Grand, T. C. (2002). Alternative forms of competition and predation dramatically affect habitat selection under foraging-predation-risk trade-offs. *Behavioral Ecology* **13**, 280-290.

Grubb, T. C. J. and Woodrey, M. S. (1990). Sex, age, intraspecific dominance status, and the use of food by birds wintering in temperate-deciduous and cold-coniferous woodlands: a review. *Studies in Avian Biology* **13**, 270-279.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology* **31**, 295-311.

Hensor, E. M. A., Godin, J.-G. J., Hoare, D. J., and Krause, J. (2003). Effects of nutritional status on the shoaling tendency of banded killifish, *Fundulus diaphanus*, in the field. *Animal Behaviour* **65**, 663-669.

Hoare, D. J., Krause, J., Peuhkuri, N., and Godin, J.-G. J. (2000). Body size and shoaling in fish. *Journal of Fish Biology* **57**, 1351-1366.

Illius, A. W. and Fitzgibbon, C. D. (1994). Costs of vigilance in foraging ungulates. *Animal Behaviour* **47**, 481-484.

- Kenward, R. E. (1978). Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *Journal of Animal Ecology* **47**, 449-460.
- Koivunen, V., Korpimäki, E., and Hakkarainen, H. (1996). Differential avian predation on sex and size classes of small mammals - doomed surplus or dominant individuals. *Annales Zoologici Fennici* **33**, 293-301.
- Kotler, B. P. and Blaustein, L. (1995). Titrating food and safety in a heterogeneous environment - when are the risky and safe patches of equal value. *Oikos* **74**, 251-258.
- Kotler, B. P., Brown, J. S., and Bouskila, A. (2004). Apprehension and time allocation in gerbils: the effect of predatory risk and energetic state. *Ecology* **85**, 917-922.
- Krause, J. and Ruxton, G. D. (2002). 'Living in groups.' (Oxford University Press: Oxford.)
- Lahti, K. (1998). Social dominance and survival in flocking passerine birds: A review with an emphasis on the Willow Tit *Parus montanus*. *Ornis Fennica* **75**, 1-17.
- Lima, S. L. (1992). Strong preference for apparently dangerous habitats-a consequence of differential escape from predators. *Oikos* **64**, 597-600.
- Lima, S. L. (1998a). Nonlethal effects in the ecological effects of predator-prey interactions- What are the ecological effects of anti-predation decision making? *Bioscience* **48**, 25-34.
- Lima, S. L. (1998b). Stress and decision making under the risk of predation: recent developments from behavioural, reproductive and ecological perspectives. *Advances in the Study of Behaviour* **27**, 215-290.
- Lima, S. L. (2002). Putting predators back into behavioral predator-prey interactions. *Trends in Ecology and Evolution* **17**, 70-75.

- Lima, S. L. and Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist* **153**, 649-659.
- Lima, S. L. and Dill, L. M. (1990). Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619-640.
- Lima, S. L., Mitchell, W. A., and Roth, T. C. (2003). Predators feeding on behaviourally responsive prey: some implications for classical models of optimal diet choice. *Evolutionary Ecology Research* **5**, 1083-1102.
- Lima, S. L. and Zollner, P. A. (1996). Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* **11**, 131-135.
- Lind, J. (2004). What determines probability of surviving predator attacks in bird migration?: the relative importance of vigilance and fuel load. *Journal of Theoretical Biology* **231**, 223-227.
- Lind, J. and Cresswell, W. (2005). Determining the fitness consequences of anti-predation behaviour. *Behavioral Ecology* **16**, 945-956.
- Lindstrom, A. (1990). The role of predation risk in stopover habitat selection in migrating bramblings. *Behavioral Ecology* **1**, 102-106.
- Mao, J. S., Boyce, M. S., Smith, D. W., Singer, F. J., Vales, D. J., Vore, J. M., and Merrill, E. H. (2005). Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Wildlife Management* **69**, 1691-1707.
- Marcstrom, V., Kenward, R. E., and Engren, E. (1988). The impact of predation on boreal tetraonids during vole cycles - an experimental-study. *Journal of Animal Ecology* **57**, 859-872.
- Martel, G. and Dill, L. M. (1995). Influence of movement by coho salmon (*Oncorhynchus kisutch*) parr on their detection by common mergansers (*Mergus merganser*). *Ethology* **99**, 139-149.

McLoughlin, P. D., Dunford, J. S., and Boutin, S. (2005). Relating predation mortality to broad-scale habitat selection. *Journal of Animal Ecology* **74**, 701-707.

Nilsson, J. A. and Christensen, B. (2000). Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos* **88**, 539-546.

Nilsson, S. G. (1984). The evolution of nest-site selection among hole nesting birds: the importance of nest predation and competition. *Ornis Scandinavica* **15**, 167-175.

Peacor, S. D. and Werner, E. E. (2001). The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceeding of the National Academy of Sciences of the United States of America* **98**, 3904-3908.

Persons, M. H., Walker, S. E., and Rypstra, A. L. (2002). Fitness costs and benefits of antipredator behaviour mediated by chemotactile cues in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *Behavioral Ecology* **13**, 386-392.

Petit, D. R. and Bildstein, K. L. (1987). The effect of group size and location within the group in the foraging behaviour of white ibises. *The Condor* **89**, 602-609.

Pettersson, L. B. and Bronmark, C. (1993). Trading off safety against food: State dependant habitat choice and foraging in crucian carp. *Oecologia* **95**, 353-357.

Pomeroy, A. C., Acevedo Seaman, D. A., Butler, R. W., Elner, R. W., Williams, T. D., and Ydenberg, R. C. (2008). Feeding-Danger Trade-Offs Underlie Stopover Site Selection by Migrants. *Avian Conservation and Ecology* **3**, 7.

Pomeroy, A. C., Butler, R. W., and Ydenberg, R. (2006). Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger. *Behavioral Ecology* **17**, 1041-1045.

Quinn, J. L. and Cresswell, W. (2004). Predator hunting behaviour and prey vulnerability. *Journal of Animal Ecology* **73**, 143-154.

- Roos, S. and Pärt, T. (2004). Nest predator affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). *Journal of Animal Ecology* **73**, 117-127.
- Rydell, J. (1998). Bat defence in lekking ghost swifts (*Hepialus humuli*), a moth without ultrasonic hearing. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**, 1373-1376.
- Schmaljohann, H. and Dierschke, V. (2005). Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*. *Journal of Animal Ecology* **74**, 138.
- Schmitz, O. J., Beckerman, A. P., and O'Brien, K. M. (1997). Behaviorally mediated tropic cascades: Effects of predation risk on food web interactions. *Ecology* **78**, 1388-1399.
- Sih, A. (1986). Antipredator responses and the perception of danger by mosquito larvae. *Ecology* **67** , 434-441.
- Sih, A., Kats, L. B., and Maurer, E. F. (2003). Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. *Animal Behaviour* **65**, 29-44.
- Sih, A., Kats, L. B., and Moore, R. D. (1992). Effects of predatory sunfish on the density, drift, and refuge use pf stream salamander larvae. *Ecology* **76**, 882-891.
- Suhonen, J. (1993). Predation risk influences the use of foraging sites by tits. *Ecology* **74**, 1197-1203.
- Turner, A. M. and Montgomery, S. L. (2003). Spatial and Temporal Scales of Predator Avoidance: Experiments with Fish and Snails. *Ecology* **84**, 616-622.
- Uetz, G. W., Boyle, J., Hieber, C. S., and Wilcox, R. S. (2002). Antipredator benefits of group living in colonial web-building spiders: the 'early warning' effect. *Animal Behaviour* **63**, 445-452.

Valeix, M., Loveridge, A. J., Chamaille-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., and Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology* **90**, 23-30.

Viscido, S. V. and Wethey, D. S. (2002). Quantitative analysis of fiddler crab flock movement: evidence for 'selfish herd' behaviour. *Animal Behaviour* **63**, 735-741.

Wahungu, G. M., Catterall, C. P., and Olsen, M. F. (2001). Predator avoidance, feeding and habitat use in the red-necked pademelon, *Thylogale thetis*, at rainforest edges. *Australian Journal of Zoology* **49**, 45-58.

Watson, M., Aebischer, N. J., and Cresswell, W. (2007). Vigilance and fitness in grey partridges *Perdix perdix* :the effects of group size and foraging-vigilance trade-offs on predation mortality. *Journal of Animal Ecology* **76**, 211-221.

Werner, E. E. and Peacor, S. D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**, 1083-1100.

Westerberg, M., Staffan, F., and Magnhagen, C. (2004). Influence of predation risk on individual competitive ability and growth in Eurasian perch, *Perca fluviatilis*. *Animal Behaviour* **67**, 273-279.

Whitfield, D. P. (2003). Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk *Accipiter nisus* predation. *Journal of Avian Biology* **34**, 163-169.

Williams, C. K., Lutz, R. S., and Applegate, R. D. (2003). Optimal group size and northern bobwhite coveys. *Animal Behaviour* **66**, 377-387.

Wooster, D. and Sih, A. (1995). A review of the drift and activity responses of stream prey to predator presence. *Oikos* **73**, 3-8.

Zuberbühler, K. and Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution* **43**, 873-886.

CHAPTER 2:

Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit?*

ALEX SANSOM¹, WILL CRESSWELL¹, JEROEN MINDERMAN² and JOHAN LIND³. (2008). *ANIMAL BEHAVIOUR* **75**, 1869-1875

¹School of Biology, University of St Andrews

²School of Biology & Psychology, Newcastle University

³Department of Zoology, Stockholm University



ABSTRACT

Animals gain anti-predation benefits from being in larger groups through increased probability of predator detection, dilution of individual risk of being attacked and confusion of predators during attack. A further benefit is that individuals in larger groups can decrease the amount of time they spend being vigilant, while maintaining a high probability of predator detection. They may then gain extra time to forage, so increasing overall intake rate. Increasing group size, however, can also increase competition so that intake rates decrease. We investigated whether there was a foraging benefit in redshanks, *Tringa totanus*, that show the group-size decrease in individual vigilance. Intake rates did not change with group size, despite an increase in time spent foraging. Interference competition increased with group size as individuals travelled more in order to find prey. Redshanks used the extra time available to forage to maintain intake rates under increased competition. Although the group size effect on vigilance did not accrue direct foraging benefits, larger groups formed, conferring other anti-predation benefits. Intake rates were maintained because the interference competition was compensated by the benefits of reduced individual vigilance.

Key words: anti-predation, group size effect, interference competition, predator detection, redshank, *Tringa totanus*

*I collected 25% of the raw data, and extracted 50% of the behavioural information from the raw video data. I carried out 100% of the analysis and 90% of the write-up with my collaborators and reviewers commenting on and correcting earlier drafts.

INTRODUCTION

Individual animals commonly decrease their vigilance in larger groups (see Elgar 1989; Lima and Dill 1990; Quenette 1990 for reviews). This inverse relationship between group size and time spent scanning the environment is often attributed to the anti-predator function of vigilance. Individuals may decrease their investment in vigilance in larger flocks due to decreased risk of predation caused by dilution, increased predator detection effects or through greater confusion of a predator during attack (Lima 1995; Roberts 1996). Even if risk does not change with group size, each individual can contribute less as more members join the group, because probability of detection is maintained by the “many eyes” effect (Pulliam 1973). This means being in a larger group has the potential to free-up time for other activities. It has been suggested that this time can be allocated to foraging and therefore another benefit of feeding in groups could be increased intake (Beauchamp 1998). Thus individuals could maximise their foraging efficiency by choosing to feed in larger groups. However, it has not often been demonstrated empirically that in larger groups the extra time available results in an individual foraging benefit (Krause and Ruxton 2002).

Competition is also affected by group size with animals in larger groups often being subject to higher levels of competition (Clark and Mangel 1986). If individuals in larger groups are foraging in a more competitive environment where food becomes scarce or aggressive interactions increase, then more attention and time will be focused on interactions with and avoiding others, searching for prey and moving to find new food sources (e.g. Cresswell 1997). As a result any extra time gained through decreased vigilance may be allocated to these activities rather than to maximizing intake rates. For example when oystercatchers feed in larger groups aggressive interactions increase causing a loss of foraging time to individuals and lowered intake (Stillman *et al.* 1997); even if individuals do not lose foraging time they still may not be able to increase their intake, for example if prey become depleted as group size increases (Selman and Goss-Custard 1988). When competition increases with group size then individuals may not necessarily accrue feeding benefits in larger flocks and may even have lower intakes in larger groups.

Here we investigate the effect of flock size on individual foraging behaviour in a natural system where individuals forage in flocks of varying size and where both vigilance and competition are likely to vary with flock size. We examine the effect of flock size on vigilance behaviour and competition to determine if birds gain any foraging benefit in larger flocks. We studied redshanks wintering at the Tynninghame Estuary in Scotland. This system has been extensively studied and previously it has been shown that redshanks in larger flocks suffer lower predation risk (through increased detection and dilution (Cresswell 1994b; Cresswell and Quinn 2004)). Redshank flocks on the salt marsh area of the estuary forage mainly on *Orchestia* sp. (Minderman *et al.* 2006; Yasué *et al.* 2003). These mobile prey items use refuges in response to redshank activity and become temporarily unavailable as more birds pass through an area causing interference competition amongst flock mates, which is reflected in lower intake rates (Minderman *et al.* 2006). As prey become unavailable and redshanks move to new areas where *Orchestia* have not yet been disturbed, a clear negative relationship between stepping rate and intake rate arises, suggesting that stepping rate is a good indicator of competition (Minderman *et al.* 2006). The redshank system is therefore ideal to investigate the effects of flock size on both time available for foraging and levels of competition. We tested whether redshanks accumulate multiple gains as flock size increases through decreased predation risk and increased foraging time, or if increased competition produces a decreased risk of predation but fewer feeding benefits.

First we confirmed that (1) individual vigilance declines with group size. Then we predicted that with increasing group size (2) time available for foraging would increase, (3) and interference competition would increase (as indicated by stepping rate). We then predicted that (4) if individuals gain foraging time, then overall intake rates would increase unless interference competition has a stronger negative effect on foraging success.

METHODS

Study Site

Observations were made at the Tynninghame estuary, Scotland, from December 2004 to February 2005 and from November 2005 to February 2006. The estuary consisted of a salt marsh (approx. 15ha), bordered by woodland and mudflats. The salt marsh

provides a feeding habitat for wintering redshanks, in particular for juvenile animals (Cresswell 1994a). Observations of foraging redshanks were conducted on birds feeding on a well-vegetated higher marsh area (approx. 10 ha) (Minderman *et al.* 2006). This area was delimited by the edge of the salt marsh on one side, and on the other side by creeks in the middle of the marsh. Flocks of redshanks foraging in this area were very active, with foraging birds moving constantly, and earlier observations in this area suggested that prey availability and the diet of redshanks consisted mostly of *Orchestia* (Cresswell 1994a; Minderman *et al.* 2006; Yasué *et al.* 2003). It has previously been shown that birds feeding in this area on the mobile *Orchestia* are affected by interference competition through temporary depression of prey availability (Minderman *et al.* 2006).

Ringling

Redshanks were caught at the start of each winter using a 5 by 15 metre whoosh net. Individuals foraging in flocks on the saltmarsh were targeted (birds feeding in other habitats tend to hold territories and feed alone (Cresswell 1994a)). All birds were ringed with a unique combination of four coloured rings above the knee (see Cresswell *et al.* 2007). Birds were caught and ringed under British trust for Ornithology (BTO) licence (permit number 4486). In the winter of 2004/5 a total of 32 redshank were ringed, in 2005/06 39 were ringed and the ringed population also included three birds surviving from the previous year.

Focal Observations

Observations of foraging colour-ringed birds were made in the winter of 2004/05 on 23 days between the 6th of December and the 8th of February and in the winter of 2005/06 on 16 days between 16th of November and 9th February. Individuals were identified using a telescope and then videoed using a Sony digital 8 video camera (x25 zoom); in 2005/06 a Sony digital video camera was used in combination with a telescope (x30 zoom) for some focals. Information on the birds' identity, time of day, flock-size, distance of the bird from predator concealing cover and position in the flock was dictated directly onto the video at the time of the observation. Flock spacing was obtained later from the video recordings. All focals lasted for one minute. An individual would not be recorded more than three or four times during a single day and focals of the same individual were never conducted consecutively whilst the bird

fed in the same flock. All birds recorded were within 150 metres of the observer, as behavioural information could not be obtained from videos of birds further away. In total we recorded 159 observations from 21 individuals in the first winter and 160 observations from 25 individuals in the second winter.

Behavioural data were extracted from the videos using JWatcherTM behavioural recording software (version 0.9 © Blumstein *et al.* 2000-2006). Videos were played back in slow motion (at a third or a fifth of the original speed depending on the camera used) and the number of pecks, swallows and steps were recorded. Vigilance behaviour was scored as head-up (above the horizontal body line), head-down (below the horizontal body line) or head horizontal (at the horizontal body line). During analysis, birds were considered to be vigilant only when in the head up posture, and non-vigilant when the head was down or horizontal. Although some level of vigilance could be maintained when the head was not up (Lima and Bednekoff 1999) the quality of information birds gained would be difficult to quantify and is likely to vary with variation in height and density of the surrounding saltmarsh grass and possible occlusion by flock mates. Also, searching and probing for *Orchestia*, an active and cryptic prey, is likely to be a very attention demanding task which suggests that probability of detecting predators is limited when redshanks have head down or horizontal body positions (Kaby and Lind 2003).

Analysis

Focal data from both winters were combined. All predictions were tested using generalised linear models (GLMMs), which were conducted using SPSS version 12.0 (SPSS, Inc., Chicago, IL, U.S.A.). Models used one response variable and possible confounding factors. In all models bird (individual) was included as a random factor (to control for variable number of focals per individual); season (2004/05 or 2005/06) and position in the flock (edge or central) were fixed factors. Time of day, time of year and time of year squared (to control for possible non-linear seasonal effects such as day length), flock details (i.e. flock size, distance to cover, flock spacing) and where relevant, behavioural variables (number of steps, pecks and swallows) were included as covariates (when not included as the response variable). In the model for stepping rate we tested for any possible non-linear effects of flock size on vigilance, and time spent foraging by including flock size squared in these models. No

interactions between covariates were considered unless they directly related to the hypothesis being tested. The response variables that were not normally distributed were transformed to normality as follows, $\ln(\text{interscan interval} + 0.01)$, arcsine (time spent foraging) and square-root (swallows per minute).

Birds that were not scanning were searching for food, so time not spent vigilant genuinely reflected time available to feed. Therefore time spent foraging was calculated as 1 minus the proportion of time spent vigilant in a focal. Swallow, pecking and stepping rates are all reported as a number per minute, distance to cover was estimated in metres, but distances between birds within a flock (flock spacing) are reported as the estimated average number of bird lengths between individuals. These were determined from the video recordings and taken as the spacing at the start of the focal, although flocks are dynamic and spacing between individuals may change during a focal. Overall flock spacing was unlikely to change significantly during the one minute period of observation.

RESULTS

In the GLMs, flock size was a significant predictor of transformed interscan interval (Table 2.1). Interscan interval increased with increasing flock size (Figure 2.1), therefore individual vigilance decreased with increasing flock size. Time spent foraging varied significantly with flock size (Table 2.2). Individuals spent a greater proportion of their time foraging as flock size increased (Figure 2.2). Stepping rate (number of steps taken in a minute) showed a significant change with flock size (see Table 2.3), with the number of steps taken per minute increasing with flock size. Stepping rate also varied significantly with flock size squared which suggests an asymptotic increase in stepping rate. This is indicative of a non-linear increase in interference competition with flock size; in larger flocks less prey are available and birds must move to new patches more rapidly to find food thus taking more steps.

Table 2.1 Prediction 1. GLM for transformed interscan interval, investigating the effect of flock size on individual vigilance.

		Type III Sum of Squares	df	F	P	b
	Intercept	0.740	1	3.94	0.048	1.314
	Intercept error	45.97	244.5			
Random:	Bird	15.6	42	1.98	0.001	
Fixed:	Position in flock	0.54	1	2.87	0.092	
	Season	1.17	1	6.25	0.013	-0.366 (2004/05)
Covariates:	Day	0.09	1	0.50	0.483	
	Day Squared	0.10	1	0.51	0.478	
	Time of day	0.06	1	0.302	0.583	
	Flock spacing	0.01	1	0.054	0.817	
	Flock size	3.80	1	20.26	<0.001	0.01
	Metres to cover	0.78	1	4.14	0.043	-0.003
	Pecks per minute	3.24	1	17.30	<0.001	0.12
	Steps per minute	3.76	1	20.06	<0.01	-0.005
	Error	45.15	241			

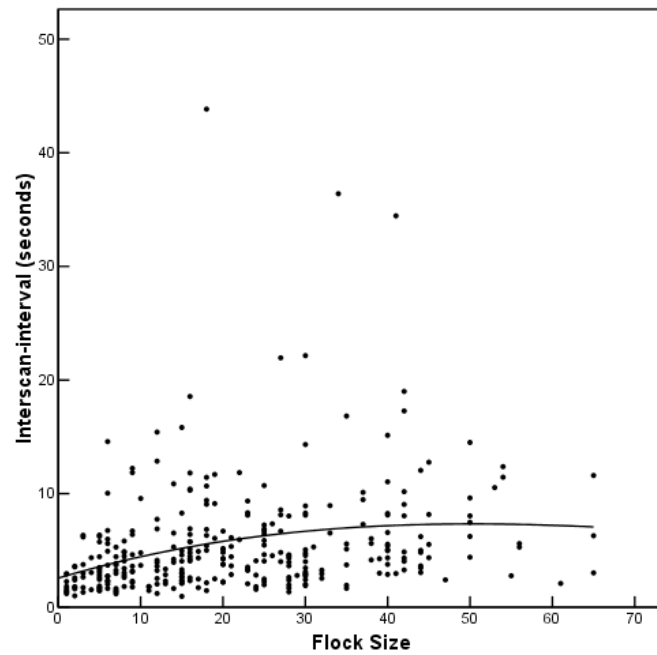


Figure 2.1. Prediction 1. Inter-scan interval increases as flock size increases. The line was fitted using curve fitting functions in SPSS to maximise variance explained, and are for illustration only to show clearly the direction and magnitude of the effect: the significance of the effects should only be assessed from the models presented in Tables 2.1-2.4.

Table 2.2. Prediction 2. GLM for transformed time spent foraging, investigating the effect of flock size.

		Type III Sum of Squares	df	F	P	b
	Intercept	0.03	1	1.0	0.317	
	Intercept error	6.74	250.8			
Random:	Bird	1.04	42	0.919	0.617	
Fixed:	Position in flock	0.10	1	3.577	0.06	
	Season	0.15	1	5.62	0.019	-0.125 (2004/05)
Covariates:	Day	0.03	1	0.926	0.337	
	Day squared	0.02	1	0.862	0.354	
	Time of day	0.13	1	4.79	0.03	0.017
	Flock spacing	0.01	1	0.364	0.547	
	Flock size	0.16	1	6.068	0.014	0.002
	Metres to cover	0.17	1	6.202	0.013	-0.001
	Pecks per minute	1.95	1	72.59	<0.001	0.009
	Error	5.6	246			

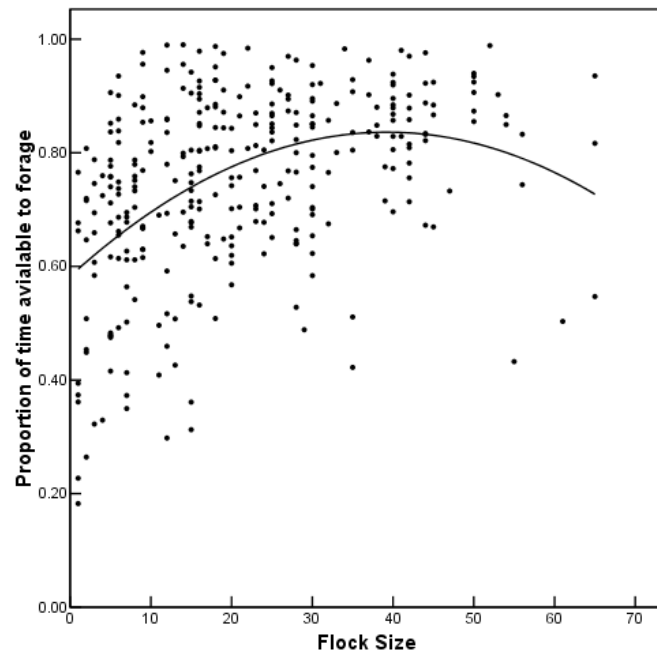


Figure 2.2. Prediction 2. The Proportion of time individuals spend foraging increases with flock size. The line was fitted using curve fitting functions in SPSS to maximise variance explained, and is for illustration only to show clearly the direction and magnitude of the effect: the significance of the effects should only be assessed from the models presented in Tables 2.1-2.4.

Table 2.3. Prediction 3. GLM for the number of steps taken in a minute, investigating the effect of flock size on the intensity of competition

		Type III Sum of Squares	df	F	P	b
	Intercept	3990.89	1	6.01	0.015	14.06
	Intercept error	168035.59	252.97			
Random:	Bird	74189.68	42	2.676	<0.001	
Fixed:	Position in flock	1930.7	1	2.925	0.088	
	Season	11164.62	1	16.92	<0.001	34.46 (2004/05)
Covariates:	Day	394.21	1	0.597	0.44	
	Day squared	9.94	1	0.015	0.902	
	Time of day	210.1	1	0.318	0.573	
	Flock spacing	31.41	1	0.048	0.827	
	Flock size	5527.74	1	8.375	0.004	1.293
	Flock size squared	3591.85	1	5.442	0.02	-0.018
	Metres to cover	5829.87	1	8.83	0.003	0.252
	Pecks per minute	15570.16	1	23.59	<0.001	-0.779
	Error	163683.5	248			

There was no significant change in intake with flock size (Table 2.4). Stepping rate and time spent foraging were both significant factors predicting intake rates. However, their effects act in opposing directions (Table 2.4). As flock size increased, the potential increase in intake from the increased time available to forage and decreased intake due to increased interference competition (reflected in stepping rate) balance each other out (see Figure 2.3). Therefore as flock size increases there was no apparent increase or decrease in intake (Table 2.4). Birds in larger flocks used the extra time available to maintain their intake under conditions where increased competition made prey harder to locate.

Table 2.4. Prediction 4. GLM for the transformed intake rate (number of swallows made in one minute), investigating the effect of flock size, stepping rate (level of competition) and time spent foraging.

		Type III Sum of Squares	df	F	P	b
	Intercept	2.9	1	13.5	<0.001	1.27
	Intercept error	54.6	249.25			
Random:	Bird	16.3	42	1.8	<0.001	0.311
Fixed:	Position in flock	0.1	1	0.4	0.508	
	Season	0.5	1	2.2	0.144	
Covariates:	Day	0.1	1	0.6	0.448	0.008
	Day squared	0.01	1	0.03	0.865	0.000
	Time of day	0.01	1	0.05	0.822	0.005
	Flock spacing	0.1	1	0.5	0.504	-0.006
	Flock size	0.001	1	0.01	0.914	-0.001
	Metres to cover	1.7	1	7.6	<0.001	-0.004
	Pecks per minute	0.3	1	1.4	0.240	0.004
	Steps per minute	5.4	1	24.6	<0.001	-0.006
	Transformed time spent foraging	2.2	1	10.1	<0.001	0.621
	Error	53.8	246			

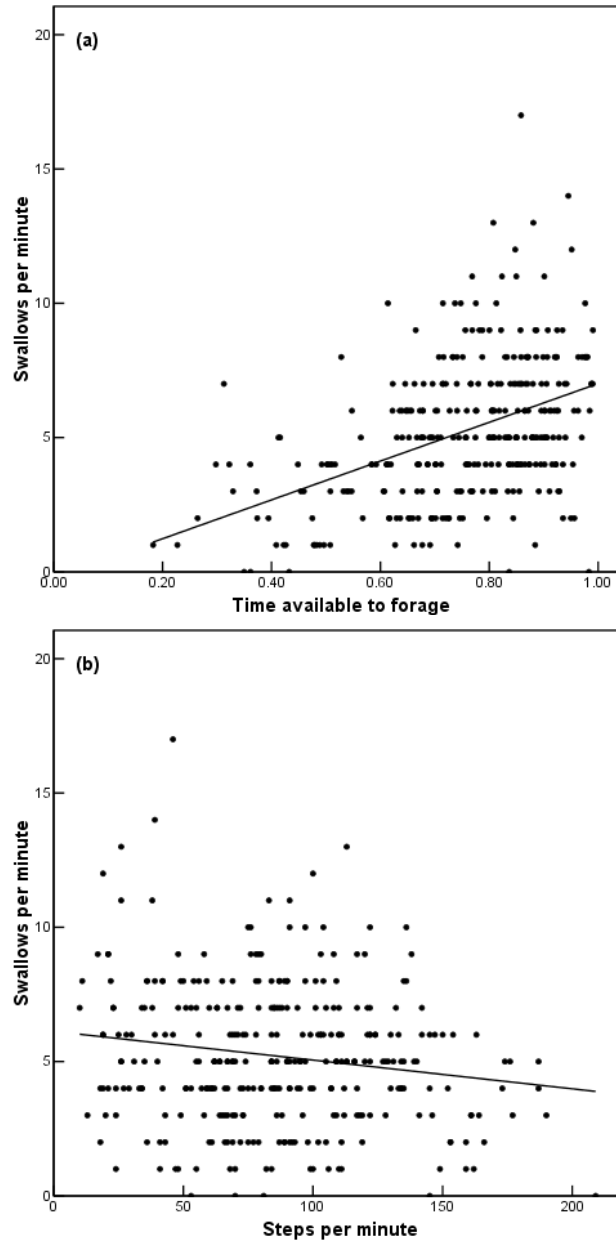


Figure 2.3. (a) Intake (swallows per minute) increases with percentage of time spent foraging and (b) decreases with increased stepping rate. Lines are linear regressions fitted through the untransformed data ($P < 0.01$ for time foraging and $P = 0.01$ for stepping rate). Using the parameter estimates from the GLM of intake rate (Table 2.4) it was calculated that the approximate decrease in intake rate (swallows per minute) due to the increased number of steps being taken of 0.39 swallows per minute (0.23-0.49, 95% confidence interval) and an increase in intake rate due to the extra time available to forage of 0.39 swallows per minute (0.10-0.76, 95% confidence interval), controlling for confounding factors. Therefore the opposing effects of competition and increased time to forage cancel out any change in intake with flock size.

DISCUSSION

When we investigated the change in vigilance with flock size we found that, as predicted, individual vigilance levels decreased with flock size. This is consistent with the majority of studies investigating the effect of flocking on vigilance (Elgar 1989; Lima and Dill 1990; Roberts 1996). Additionally vigilance has previously been found to decrease with flock size in this system (Cresswell 1994b). As predicted, we found that individuals spent more time foraging as flock size increased. When investigating the effect of flock size on competition we found that competition also increased with flock size, which was indicated by a significant increase in stepping rate with flock size. With increasing flock size, foraging redshanks moved between food patches more quickly because disturbance decreases prey availability as more birds pass through an area (Minderman *et al.* 2006).

The increase in the proportion of time spent foraging does not appear to translate into a foraging benefit, because redshanks show no change in intake with flock size. The lack of a foraging benefit is not consistent with many other studies investigating the effect of decreased vigilance on intake. In a review (Beauchamp 1998) (looking at mean food intake, not individuals) found that out of 40 studies where vigilance decreased as a function of group size only 8 showed no change in intake. However, when competition also increases with flock size, then this may limit intake and has the potential to cause a decrease in intake with flock size (Caraco 1979), often because individuals lose foraging time when interacting with others (Ens and Goss-Custard 1984; Stillman *et al.* 1997). We have demonstrated in this case that individuals gain foraging time as flock size increases. However the decrease in prey availability as flock size increases has the potential to lower the intakes of birds in larger flocks (Minderman *et al.* 2006). Prey disturbance has previously been suggested as a potential cause of decreased intake with flock size (Beauchamp 1998) operating in a similar way to prey depletion, but it has not often been demonstrated empirically. However, in a similar result to this study (Petit and Bildstein 1987) found that white ibis *Eudorimus albus* foraging at the centre of flocks spent more of their time foraging but did not increase their intake due to disturbance of their crab prey, by other flock members. We found that as flock size increased individuals were able to maintain their intake despite the fact that increased competition made prey harder to locate.

When in larger flocks individuals are able to put more effort into foraging as is reflected in the increased proportion of time spent on this activity, however any potential gains in intake are constrained by interference competition. Our results then suggest that the main function of flocking redshanks in this system is to reduce predation risk, rather than to gain foraging benefits. The extra time available to forage that occurs in larger groups means that individuals can gain the antipredation benefits of being in a larger flock without incurring the full costs of competition. This may result in flocks that are larger than would otherwise be sustainable; thus providing a less risky feeding environment where individuals do not need to compromise their safety to maintain their intake. This may be particularly important in redshanks because they do not accumulate significant energy reserves (Mitchell *et al.* 2000) and so are constantly under pressure to maintain their intake rates in order to meet their energy budget.

Our results suggest that an ‘optimal’ group size in terms of the trade-off between food and safety, which has been suggested and demonstrated previously for group foraging animals (Higashi and Yamamura 1993) is not seen in this case since individuals maintain the same intake across flock sizes. It may be that individual redshanks seek to forage in the largest possible groups in order to minimise their predation risk. However, when large numbers of birds are present flocks might reach a maximum size at the point at which the balance between the positive effect of increased time available to forage and the negative effect of competition breaks down and intake rates cannot be maintained. This seems likely as individual redshanks will still have to spend a certain proportions of their time scanning for predators and therefore will reach a point where they cannot dedicate any more time to foraging; also given that competition depresses prey availability over a large area at very high levels of competition (i.e. large flock sizes) all patches are likely to become unprofitable.

Our results also provide another example of how flock dynamics could also be influenced by individual competitive ability (Rowcliffe *et al.* 2004) and its interaction with competitor density (Cresswell 1998a) prey availability (Cresswell 1998b) and patch conditions (Cresswell *et al.* 2001). Individuals better able to cope with high levels of competition may be able to utilise the extra foraging time to gain a higher intake in larger flocks as well as the antipredator benefits, whereas less competitive

redshanks may only gain antipredator benefits and may not be able to maintain their intake rate in larger flocks. The role of individual variation in competitive ability and other behaviours such as vigilance are therefore likely to be important in determining individual decisions about which flock to feed in and when to leave a flock.

Interference competition is frequently neglected in studies of vigilance and its influence in the evolution of social behaviour, but as our redshank system shows, it is probably crucial in understanding the costs of social behaviour, and this seems likely to apply more generally.

ACKNOWLEDGMENTS

We thank John Quinn, Ross Macleod, Mark Hulme, Bobby Anderson, Emma and Alva Ehn, Jeroen Minderman, East Lothian District Council, and the Tynninghame Estate for logistical help. We also thank F.S Dobson and an anonymous referee whose comments helped substantially to improve a previous version of this article. AS was supported by a NERC studentship to WC, WC is a Royal Society University Research fellow, JM was supported by a grant from the Marco Polo University Fund and JL was funded by the Swedish Research Council.

REFERENCES

- Beauchamp, G. (1998). The effect of group size on mean food intake rate in birds. *Biological Reviews of the Cambridge Philosophical Society* **73**, 449-472.
- Caraco, T. (1979). Time budgeting and group size: a theory. *Ecology* **60**, 611-617.
- Clark, C. W. and Mangel, M. (1986). The evolutionary advantages of group foraging. *Theoretical Population Biology* **30**, 45-75.
- Cresswell, W. (1994a). Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *Journal of Animal Ecology* **63**, 589-600.
- Cresswell, W. (1994b). Flocking is an effective anti-predation strategy in Redshanks, *Tringa totanus*. *Animal Behaviour* **47**, 433-442.

- Cresswell, W. (1997). Interference competition at low competitor densities in blackbirds *Turdus merula*. *Journal of Animal Ecology* **66**, 461-471.
- Cresswell, W. (1998a). Relative competitive ability changes with competitor density: evidence from feeding blackbirds. *Animal Behaviour* **56**, 1367-1373.
- Cresswell, W. (1998b). Variation in the strength of interference competition with resource density in blackbirds, *Turdus merula*. *Oikos* **81**, 152-160.
- Cresswell, W., Lind, J., Quinn, J. L., Minderman, J., and Whitfield, D. P. (2007). Ringing or colour-banding does not increase predation mortality in redshanks *Tringa totanus*. *Journal of Avian Biology* **38**, 309-316.
- Cresswell, W. and Quinn, J. L. (2004). Faced with a choice, predators select the most vulnerable group: implications for both predators and prey for monitoring relative vulnerability. *Oikos* **104**, 71-76.
- Cresswell, W., Smith, R. D., and Ruxton, G. D. (2001). Absolute foraging rate and susceptibility to interference competition in blackbirds varies with patch conditions. *Journal of Animal Ecology* **70**, 228-236.
- Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the evidence. *Biological Review* **64**, 13-33.
- Ens, B. J. and Goss-Custard, J. D. (1984). Interference among oystercatchers, *Haematopus ostralegus* feeding on mussels *Mytilus edulis*, on the Exe estuary. *Journal of Animal Ecology* **53**, 217-231.
- Higashi, M. and Yamamura, N. (1993). What determines animal group size? Insider-outsider conflict and its resolution. *American Naturalist* **142**, 553-563.
- Kaby, U. and Lind, J. (2003). What limits predator detection in blue tits (*Parus caeruleus*): posture, task or orientation? *Behavioral Ecology and Sociobiology* **54**, 534-538.

Krause, J. and Ruxton, G. D. (2002). 'Living in groups.' (Oxford University Press: Oxford.)

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour* **49**, 11-20.

Lima, S. L. and Bednekoff, P. A. (1999). Back to basics of antipredatory vigilance: can nonvigilant animals detect attack? *Animal Behaviour* **58**, 537-543.

Lima, S. L. and Dill, L. M. (1990). Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619-640.

Minderman, J., Lind, J., and Cresswell, W. (2006). Behaviourally mediated indirect effects: interference competition increases predation mortality in foraging redshanks. *Journal of Animal Ecology* **75**, 713-723.

Mitchell, P. I., Scott, I., and Evans, P. R. (2000). Vulnerability to severe weather and regulation of body mass of Icelandic and British Redshank *Tringa totanus*. *Journal of Avian Biology* **31**, 511-521.

Petit, D. R. and Bildstein, K. L. (1987). The effect of group size and location within the group in the foraging behaviour of white ibises. *The Condor* **89**, 602-609.

Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology* **38**, 419-422.

Quenette, P. Y. (1990). Functions of Vigilance in mammals: a review. *Acta Oecol.* **11**, 801-818.

Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour* **51**, 1077-1086.

Rowcliffe, J. M., Pettifor, R. A., and Carbone, C. (2004). Foraging inequalities in large groups: quantifying depletion experienced by individuals in goose flocks. *Journal of Animal Ecology* **73**, 97-108.

Selman, J. and Goss-Custard, J. D. (1988). Interference between foraging redshanks *Tringa totanus*. *Animal Behaviour* **36**, 1542-1544.

Stillman, R. A., Goss-Custard, J. D., and Caldow, R. W. G. (1997). Modelling interference from basic foraging behaviour. *Journal of Animal Ecology* **66**, 692-703.

Yasué, M., Quinn, J. L., and Cresswell, W. (2003). Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in redshanks. *Functional Ecology* **17**, 727-736.

CHAPTER 3:

Individual behaviour and survival: the roles of predator avoidance, foraging success and vigilance.*

ALEX SANSOM¹, JOHAN LIND², WILL CRESSWELL¹. (2009). *BEHAVIORAL ECOLOGY IN PRESS*

¹School of Biology, University of St Andrews

²Department of Zoology, Stockholm University



ABSTRACT

Variation in anti-predation behaviour should translate into variation in survival. Effective general defences, such as predator avoidance, decrease the likelihood that an individual is attacked and should therefore reduce selection on behaviours that enhance probability of escape on attack. Escape behaviours become important if animals cannot avoid attack. We investigated the relative effects of avoidance and escape enhancing behaviours on the survival of juvenile redshanks, *Tringa totanus*, over two winters. We predicted that avoidance behaviour should be the primary behavioural correlate of survival, but when forced, by starvation risk, into areas where risk of attack is much higher, behaviours that reduce risk of capture once attacked should also promote survival. We found that reducing exposure to attack was most important for increasing survival and that increased vigilance and foraging success rate only increased survival for individuals that spent more time in high-risk areas. Use of the high-risk area and survival varied between years, suggesting that variation in starvation risk (i.e. colder winters) may provide a mechanism for selection on “capture reducing” anti-predation behaviours to be maintained because predator avoidance, the most effective anti-predation behaviour, is not then possible.

Keywords: Predation risk, avoidance, vigilance, foraging efficiency, survival

*I collected 50% of the raw data, and extracted 50% of the behavioural information from the raw video data. I carried out 100% of the analysis and 80% of the write-up with my collaborators and reviewers commenting on and correcting earlier drafts.

INTRODUCTION

Predation risk is a major selective force shaping animal behaviour (see Lima and Dill 1990; Lima 1998b and Caro 2005 for reviews). Within populations, individual variation in behaviour is often recorded (Sih *et al.* 2004). If this variation occurs in behaviours that affect predation risk then individuals may also vary in terms of their survival (Lind and Cresswell 2005). An animal whose behaviour reduces its risk of predation is more likely to survive to breed, and therefore have increased fitness, but different anti-predation behaviours have different effects. The wide variety of behaviours which reduce predation risk can be considered as lying on a continuum from very broad scale behaviours such as choice of habitat and activity level - which act through avoidance to reduce predation risk - to very specific behaviours which reduce risk of capture when attacked - such as angle of an escape response flight (Lima and Dill 1990; Caro 2005).

Selection on avoidance behaviours that limit exposure to attacking predators may be strong, because individuals successfully avoiding attack effectively eliminate predation risk (Lima 1998a; Mao *et al.* 2005; Valeix *et al.* 2009). Such behaviours should therefore account for much of the variation in individual survival. Evidence suggests that foraging individuals often avoid areas with a high risk of attack (Gilliam and Fraser 1987; Fraser *et al.* 1995; Abramsky *et al.* 1996; Watts 1991; Sparrevik and Leonardsson 1995; Krams 1996; Rochette and Dill 2000; Altendorf *et al.* 2001) even at a cost to energetic gains (Hilton *et al.* 1999b; Lima 1990; Cresswell 1994a; Todd and Cowie 1990; Kohler and McPeck 1989; Walther and Gosler 2001). However, completely escaping detection by predators, or always avoiding predator hunting areas, is often incompatible with other essential activities such as foraging (Dill 1990). When ecological conditions make the cost of predator avoidance high, individuals must accept a level of predation risk in order to meet their energy budget (Brown and Kotler 2004). Under these circumstances, when individuals become frequently exposed to attack, more specific defences such as vigilance also play a role in survival and thus will also affect individual fitness. Where escape behaviours are particularly effective, then animals may forage in areas with high attack rates and so do not have to use avoidance behaviour (Lima 1992; Heithaus *et al.* 2009).

Most foraging animals achieve their energy budget whilst coping with predation risk by balancing avoidance of attacking predators (when possible) with reducing risk via defence behaviours when exposed to risk of attack (Lind 2004). The relative effect of very general and more specific anti-predation behaviours on survival should be related to the point at which risk is reduced (Lima and Dill 1990). Behaviours that eliminate or greatly reduce risk of attack increase survival without recourse to any behaviours that reduce probability of capture on attack, but once an individual is exposed to attack, such escape enhancing behaviours become important in predicting survival. Predator avoidance mechanisms and escape behaviour mechanisms are therefore under different selective regimes and the evolution of one type of prey survival mechanism reduces selection on the other (Brodie and Formanowicz 1991).

Resolving the relative importance of avoidance and escape enhancing defences in terms their effects on survival and fitness – and therefore the strength of selection on them – is likely to be key to a better understanding of predator-prey relationships and the ecosystems in which they operate (Cresswell 2008). For example, non-lethal effects of predation risk, such as habitat shifting to avoid risk, can determine the structure of ecosystems (Agrawal 2001), affecting both predator hunting strategies and prey choice (e.g. Durant 2000; Sergio *et al.* 2003). Additionally, the co-evolution of predator-prey species pairs can only occur or be predicted when predators and prey actually interact and therefore avoidance by prey has not been achieved (e.g. see Caro 1995). Gaining such insights into predator prey relationships is difficult unless the full range of possible anti-predation behaviours are studied in context (Lind and Cresswell 2005).

We investigated the effect of different anti-predation behaviours on the survival of juvenile redshanks, *Tringa totanus*, over-wintering on a Scottish estuary. In our system individuals must trade off energetic gains against predation risk (Cresswell 1994a) from both Sparrowhawks *Accipiter nisus* and Peregrines *Falco peregrinus* (Cresswell and Whitfield 1994). Individuals can forage on mud flats where they feed widely spaced from each other, are often territorial and are far from predator concealing cover. Predator attack rate and hunting success is low (Cresswell 1994a), because distance from cover (>100m) ensures a high probability of early detection of an approaching predator, even by single individuals (Quinn and Cresswell 2004).

Foraging on the mudflats is relatively unprofitable (Yasué *et al.* 2003). Therefore, although individuals can reduce their predation risk by avoidance of attacking predators they must accept lower foraging gains. However, in order to meet their energy budget during cold weather, individuals also forage close to predator concealing cover (<100m) on an area of saltmarsh where prey is highly profitable, but where predator attack rate is high (Cresswell 1994a; Yasué *et al.* 2003). During these periods individuals must rely on behaviours that prevent capture when attacked, rather than simple avoidance behaviours that reduce their risk of attack, as on the mudflats. Potentially, individuals can reduce their risk of capture through vigilance, group size and position within a group (relative to cover and other individuals) (Cresswell 1994b; Cresswell and Quinn 2004; Hilton *et al.* 1999b; Quinn and Cresswell 2005; Quinn and Cresswell 2006). We therefore have a system where juvenile redshanks spend their time foraging away from areas with a high risk of attack, if possible. When risk of starvation is high individuals may spend several hours a day feeding on the profitable saltmarsh, where attacks are very likely. As a consequence, detection and escape behaviours that reduce probability of capture on attack are likely only to be important in reducing predation risk if, and when, individuals feed on the saltmarsh.

We attempt to determine the relative effects of avoidance of attack (a general risk reducing behaviour) and more specialized anti-predator behaviours (which reduce capture probability once attacked) on survival time. We predict that individuals that reduce predation risk by avoiding attack will have longer survival times, and variation in secondary, capture reducing behaviours will not affect survival. Individuals that spend large amounts of time in the high attack rate area will have shorter survival times, but can increase their survival via behaviours that reduce risk of capture on attack, such as vigilance, spacing, and position within the flock. Although flock size is also an important determinant of capture risk we only consider it as a confounding variable, because flock size was limited for individuals: individual redshanks often had no choice of flock size with only one flock available on any day, and there was little variation in flock size between sampling days.

METHODS

Study Site

Observations were made at the Tynninghame estuary, Scotland, from December 2004 to February 2005 (first winter) and from November 2005 to February 2006 (second winter). The estuary consisted of an area of saltmarsh bordered on two sides by woodland, and an adjoining mud flat (Yasué *et al.* 2003). Redshanks foraging on the saltmarsh fed in flocks and mainly on energy rich *Orchestia sp.* (Yasué *et al.* 2003; Minderman *et al.* 2006); flocks were often less than 50m to cover and are exposed to high risk of attack by predators (Cresswell 1994a). Redshanks foraging on the mud flat were more widely spaced with individuals often holding territories and foraging alone. On the mud individuals usually feed above 100m and frequently above 200m from cover and foraged on less energy rich prey such as *Corophium*; they were exposed to a lower risk of attack (Cresswell 1994a; Yasué *et al.* 2003). During periods of cold weather juvenile redshanks are frequent visitors to the saltmarsh, because they are unable to meet their energy budget foraging only on the mud flat (Cresswell 1994a; Yasué *et al.* 2003). Individuals spend a variable number of hours each day feeding in this high profitability, high-risk area. Adults were rarely observed spending time foraging on the saltmarsh. All individuals were forced onto the saltmarsh on a regular basis when the mud flat area is covered by the high tide, although they do not necessarily forage at this time.

Ringling

Redshanks were caught at the start of each winter using a 5 by 15 meter whoosh net. Individuals foraging in flocks on the saltmarsh were targeted (birds feeding in other habitats tend to hold territories and feed alone (Cresswell 1994a): 32 individuals were colour ringed in the first winter and 38 in the second winter. All birds were ringed with a unique combination of four colour rings above the knee (see Cresswell *et al.* 2007). Birds were caught and ringed under a British Trust for Ornithology (BTO) license (permit number 4486).

Focal Observations

All observations of foraging redshanks were conducted on juvenile birds feeding in flocks on a well-vegetated higher marsh area (approx. 10 ha) (Minderman *et al.* 2006). All focals lasted for one minute and no focals were conducted during high tide

periods. Individuals were identified using a telescope and then videoed using a Sony digital 8 video camera (x25 zoom); in 2005/06 a Sony digital video camera was used in combination with a telescope (x30 zoom) for some focals. Information on the birds' identity, flock-size and position in the flock (central, edge furthest from predator-concealing cover, edge closest to cover) was dictated directly onto the video at the time of the observation. Flocks were defined as a distinct group of redshanks foraging coherently in the same direction, with each individual being a similar distance (no more than a few meters) from its nearest neighbour. Flock sizes remained relatively stable over time, however if additional redshanks joined a flock during a focal observation it would be abandoned and restarted later. An individual was not recorded more than three or four times during a single day and focals of the same individual were never conducted consecutively whilst the bird fed in the same flock. All birds recorded were within 150m of the observer, as behavioural information could not be obtained from videos of birds further away. Observations of foraging colour-ringed birds were made in the winter of 2004/05 on 23 days between the 6th of December and the 8th of February and in the winter of 2005/06 on 16 days between 16th of November and 9th February. In total, over two winters of sampling, we collected focal data from 43 individuals with a mean of 6.91 ± 0.87 focals per bird. On days that we collected focal data, we collected 1.8 ± 0.03 focals, per bird per day.

Behavioural data were extracted from the videos using JWatcherTM behavioural recording software (version 0.9 © Blumstein *et al.* 2000-2006). Videos were played back in slow motion (at a third or a fifth of the original speed depending on the camera used). Distance of the focal bird from its nearest neighbour was estimated in bird-lengths at the start of each focal. Vigilance behaviour was scored as head-up (above the horizontal body line), head-down (below the horizontal body line) or head-horizontal (at the horizontal body line). During analysis, birds were considered to be vigilant only when in the head-up posture, and non-vigilant when the head was down or horizontal. Although some level of vigilance could be maintained when the head was not up (Lima and Bednekoff 1999) the quality of information gained by the birds would be difficult to quantify and is likely to vary with variation in height and density of the surrounding saltmarsh grass and possible occlusion by flock mates. Also, searching and probing for *Orchestia* sp., an active and cryptic prey, is likely to be a very attention demanding task which suggests that probability of detecting predators

is limited when redshanks have head-down or head-horizontal body positions (Kaby and Lind 2003).

Measuring behaviour

Individuals were only considered for analysis if five or more one-minute focal observations had been collected. There were no significant relationships found between the number of focals a bird had and values for behaviours. Values were calculated for individual behaviours using information from all focals as follows: vigilance was considered as the mean proportion of time an individual spent being vigilant (head up) per minute; mean foraging success was calculated as the mean number of pecks/number of swallows per minute; nearest neighbour distance was the mean of the distances of an individual from its nearest neighbour at the start of each focal. We also calculated the proportion of focals in which an individual was on the edge closest to predator concealing cover within a flock. Our observations of flocks suggest that flock size and structure remained stable enough over a one minute for this to accurately represent the position of an individual over the focal period. We obtained full (i.e. more than five focals) behavioural data from 13 individuals in 2004/05 and 13 in 2005/6. These individuals were focal sampled on the saltmarsh on a mean of 6.27 ± 0.56 days.

Estimating time spent on the saltmarsh

On days when observations were being collected an observer was present at the saltmarsh throughout the day. Regular scans were made for colour-ringed birds, and if present focals would be collected and the time of day would be noted. The individuals for which we collected sufficient behavioural data all used the saltmarsh regularly; this means our sample is necessarily biased towards birds that fed on the saltmarsh on a daily basis because these were the individuals that we could regularly sample. We therefore test how survival was affected by avoidance behaviour and/or capture-risk reducing behaviours on a subset of individuals that used the risky saltmarsh more or less daily. Our estimate of avoidance is each individual's degree of daily use of the saltmarsh.

To assess the relative amount of time each individual spent on the saltmarsh within each day we first counted the number of 'whole days' each individual spent on the

saltmarsh (i.e. number of times it was seen in both the morning and afternoon of the same day). We then counted the total number of days when an individual was seen only in the morning or in the afternoon. An index of relative time spent on the saltmarsh was then calculated as follows: $\text{Index} = \frac{\text{Number of 'whole days' seen}}{\text{Number of 'whole days' seen} + \text{Number of days seen only in the morning} + \text{Number of days seen only in the afternoon}}$. A bird that spent all day on the saltmarsh would have a higher value of proportionate use of the saltmarsh compared to one that used the saltmarsh for short periods. This method also removes any bias due to longer-living birds having more potential to be seen on the saltmarsh over the whole winter.

Measuring survival

Redshanks are typically site faithful during winter (Burton 2000; Cresswell and Whitfield 1994) and no bird was reported outside the estuary in either year so a bird no longer seen is not likely to have moved outside of the study site. Additionally, regular searches of woodland adjacent to the saltmarsh were conducted for sparrowhawk kills (see Cresswell 1995). We found that the ratio of ringed to un-ringed kills closely matched the ratio of ringed to un-ringed birds in the population, indicating that the population was likely to be sedentary and that decreases in colour-ringed birds accurately reflected mortality from sparrowhawks (Cresswell *et al.* 2007). Seven individuals (22% of all colour-ringed birds) in 2004/05 and eight (20%) in 2005/6 that were noted as “disappeared” were subsequently found dead due to sparrowhawk predation immediately adjacent to the saltmarsh. Higher intensity searches for kills from all raptor species over the entire estuary in previous years have shown that almost all redshanks that disappear can be recovered as raptor kills or (very rarely) starved carcasses within a few hundred meters of the estuary (Cresswell and Whitfield 1994), and both winters of this study were similar to years of intensive searches in terms of observed sparrowhawk and peregrine attack and kill rate.

If a focal redshank disappeared we were reasonably confident that it had been killed. The individuals that we sampled were regular visitors to the saltmarsh and all individuals that are included in the analyses in this paper fed on the saltmarsh, on average, every other day. The average gap between sampling days between consecutive sightings of the focal individuals was 1.3 ± 0.3 days for the first winter (N=13 birds, average minimum 0.3 days and average maximum 3.1 days) and $1.7 \pm$

0.5 days for the second winter (N=13 birds, average minimum 0.2 days and average maximum 6.4). When an individual was foraging on the saltmarsh it was relatively conspicuous and frequently moved to different areas of the saltmarsh ensuring a high chance of detection. The probability of seeing an individual redshank on any of the sampling days between the start of the study and the end of the study was 0.42 ± 0.07 in winter 1 (N=23 days) and 0.34 ± 0.05 in winter 2 (N=16 days). The probability of seeing an individual redshank on any of the sampling days between the start of the study and the last day that an individual was sighted (i.e. now accounting for when we believe death occurred) was 0.48 ± 0.06 in winter 1 and 0.45 ± 0.04 in winter 2. All individuals in both years were assumed to be alive on the 14th of November (the earliest date of observations) as all birds were seen alive at this time or were ringed after this. Time to death was calculated as the time from this date until the last day known to be alive or for surviving individuals until the last day of focal observations.

We used a Cox proportion hazards model for the time to death data (Cox 1972), since this incorporates censored data (thus accounting for individuals that survived) and can be used when risk is non-uniform over time (which is likely to be the case with predation risk over the winter period – (Quinn and Cresswell 2004). In model 1, behavioural data and time spent on the saltmarsh were included as continuous covariates to test if avoidance behaviour determined survival, and year was included as a categorical variable to investigate potential differences in survival between years. Although our data were not sufficient to test properly for the effect of flock size choices on survival, we included mean size of flock for each individual to control for its potential confounding effects. This is due to the potential effects flock size may have on vigilance (Cresswell 1994b), flock spacing (Quinn and Cresswell 2006) and foraging success (Minderman *et al.* 2006). None of the behavioural variables were found to be significantly time dependant. In model 2 we tested the interactions between time spent on the saltmarsh and other behaviours to investigate the effects of secondary escape behaviours on survival. Analysis was conducted using SPSS version 12.0 (SPSS, Inc., Chicago, IL, U.S.A.). We present both full models and minimal models derived using a backward stepwise selection process: the former to demonstrate that our results are robust regardless of the subjectivity inherent in backwards deletion (Whittingham *et al.* 2006), and the latter to maximize the statistical power in models of limited sample size.

RESULTS

Model 1: individual survival is primarily determined by avoidance of risky areas

We found that individual survival was significantly affected by time spent in the habitat with high risk of attack (see Table 3.1); individuals that spent relatively less time on the saltmarsh survived for longer (Figure 3.1a). In the minimal model survival also differed significantly between years, being lower in the second winter (see Table 3.1 and Figure 3.1b). None of the other behaviours we included in Model 1 significantly affected survival.

Table 3.1. Cox proportional hazards model of individual survival time in days investigating the effects of anti-predation behaviour, controlling for the effect of year, showing parameter estimates and standard errors. Critical values for both the full and minimal model are given. Significant P values are marked in bold.

Variable	df	b	se	Full model		Minimal model	
				Wald	p	Wald	p
Foraging success	1	7.3	18.8	0.15	0.70		
Vigilance	1	5.1	6.1	0.71	0.40		
Nearest Neighbour	1	-0.045	0.144	0.10	0.75		
Probability of being close to cover	1	-2.3	1.7	1.89	0.17		
Flock size	1	0.047	0.07	0.46	0.50		
Time on Saltmarsh	1	4.3	1.8	5.43	0.02	7.09	<0.01
Winter	1	-1.2	0.9	1.87	0.17	5.31	0.02

Model 2: individual survival in high-risk areas is determined by foraging and vigilance

When considering the secondary effects of behaviour on survival we found that time on the saltmarsh and year both still affected survival in the same way. However we also found interaction terms to be significant for vigilance and foraging success, suggesting a role for other anti-predation behaviours in survival (Table 3.2). Figure 3.2 shows that for individuals that spent relatively more time on the saltmarsh, survival time increased with increased vigilance and foraging success, whereas survival of individuals spending less time on the saltmarsh was not significantly affected by these behaviours. There was a significant interaction between foraging success and vigilance suggesting that only individuals that maintained a high level of

vigilance whilst having a high foraging success gained a survival advantage. Position in the flock and nearest neighbour distance did not affect survival.

Table 3.2. Cox proportional hazards model of individual survival time in days investigating the effects of anti-predation behaviour including interactions between time spent exposed to risk, vigilance and foraging success, controlling for the effect of year, showing parameter estimates and standard errors. Critical values for both the full and minimal model are given. Significant P values are marked in bold.

Variable	df	b	se	Full model		Minimal model	
				Wald	P	Wald	p
Foraging success	1	941.2	317.8	8.77	<0.01	9.80	<0.01
Vigilance	1	409.1	143.7	8.09	<0.01	8.81	<0.01
Nearest Neighbour	1	0.002	0.139	0.00	0.99		
Probability of being close to cover	1	4.5	3.0	2.31	0.13		
Time on Saltmarsh	1	90.2	29.1	9.62	<0.01	8.30	<0.01
Winter	1	-5.7	1.8	9.75	<0.01	9.01	<0.01
Flock size	1	0.283	0.10	6.75	0.01	5.25	0.02
Time on Saltmarsh*Vigilance	1	-173.232	68.3	6.43	0.01	5.38	0.02
Foraging success*Vigilance	1	-3537.0	1244.2	8.08	<0.01	8.86	<0.01
Time on Saltmarsh*Foraging success	1	-460.5	189.5	5.90	0.02	5.10	0.02

Interactions of nearest neighbour and probability of being close to cover with time on the saltmarsh were removed for clarity, because they were not significant (B=5.944 P=0.058 and B=21.274 P=0.102 respectively) and the significance of other effects were unchanged by this.

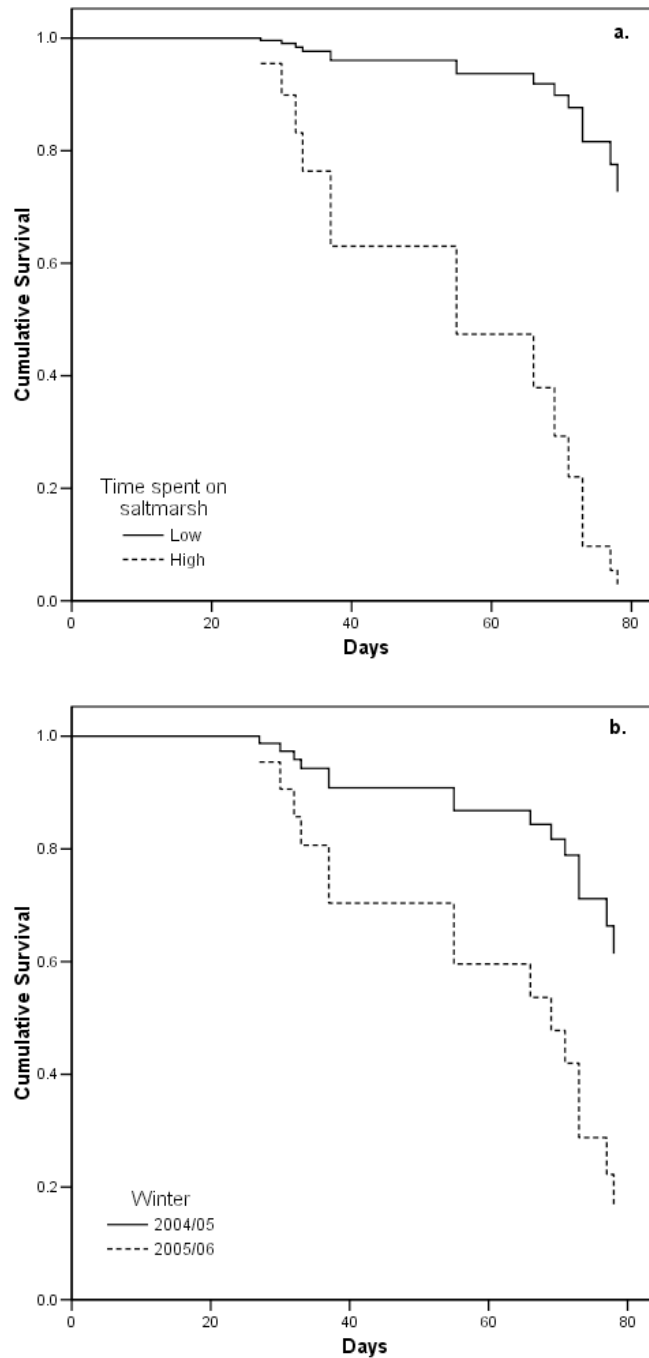


Figure 3.1. Cox proportional hazards survival functions (a) comparing survival of individuals spending relatively more time feeding in the risky saltmarsh habitat to individuals spending less time there (b) comparing survival of individuals in different winters. Time on the saltmarsh was modelled as a continuous variable, but here a split between ‘high’ and ‘low’ saltmarsh usage is based on individual values either being above or below the overall mean of time on the saltmarsh. This split was made purely to illustrate the relative effect spending more time on the saltmarsh has on cumulative survival.

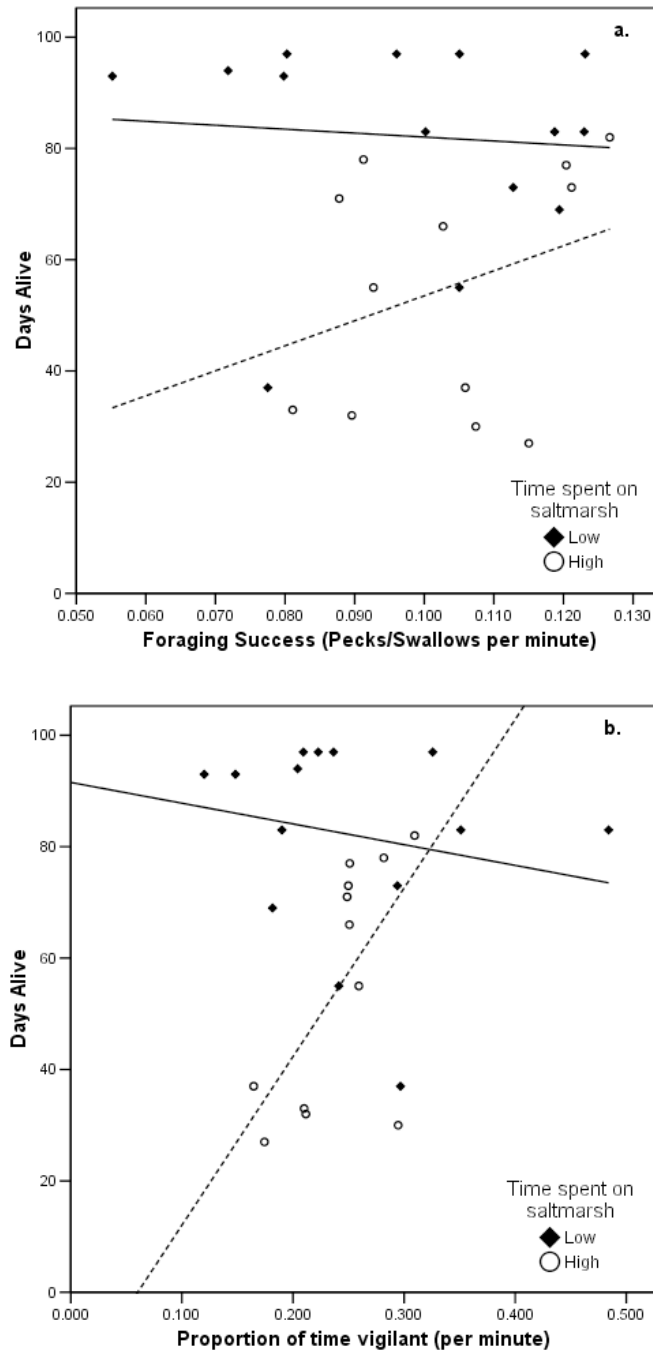


Figure 3.2. The effect of foraging success (a) and vigilance (b) on survival time in days for individuals spending relatively more time feeding in the risky saltmarsh habitat to individuals spending less time there. Lines are linear regressions fitted to the data, (a) high proportion of time spent on the saltmarsh: $R^2=0.10$, low proportion of spent time on the saltmarsh: $R^2=0.01$; (b) high proportion of time spent on the saltmarsh: $R^2=0.39$, low proportion of time spent on the saltmarsh: $R^2=0.04$. The split between 'high' and 'low' saltmarsh usage was calculated as for Figure 3.1 and again is arbitrary to illustrate the relative effect of spending more time on the saltmarsh.

DISCUSSION

We found that juvenile redshanks able to minimize time spent foraging on the predator-exposed saltmarsh gained a survival advantage irrespective of their vigilance and foraging behaviour. However, individuals spending relatively more time in a high-risk environment showed increased survival times with increased vigilance and intake rate. Position in a flock had no effect on survival. These results suggest that avoidance behaviour primarily affects survival, and behaviours that promote escape on attack only become relatively important to survival when avoidance behaviours are not possible.

The effect of foraging in a risky environment in this system, in terms of reduced survival, suggests there may be strong selection on individual juvenile redshanks to use avoidance as a primary defence against predation risk. This selective pressure produces a non-lethal effect of predation risk (Cresswell 2008; Lima 1998a), whereby individuals should feed away from predators when possible, causing an overall redistribution of the population to safer but less profitable habitats (Cresswell 1994a; Cresswell and Whitfield 2008). Evidence for such non-lethal effects of predators on habitat use by individuals and populations has previously been found mainly in aquatic or invertebrate systems (Werner and Peacor 2003; Wooster and Sih 1995). However, the selective pressure to avoid predators and the resultant ‘non-lethal’ effects of predation risk on individual foraging decisions are likely to play an important role in shaping a wide range of predator-prey communities; for example avoidance by one prey type may force predators to select alternative prey or to alter their hunting strategy and may strongly effect whole ecosystems through cascading trophic effects (Lima 1998a; Cresswell 2008).

For individuals that spent relatively more time exposed to a high risk of attack, vigilance also increased survival. This finding is supported by previous work which has shown that vigilance improves the chance of predator detection and escape (Hilton *et al.* 1999a; Quinn and Cresswell 2005). Higher levels of individual vigilance have also previously been linked with increased survival in other species (Stuart-Smith and Boutin 1995; Watson *et al.* 2007). We also found that a high foraging success rate promoted survival. It is possible that only individuals with high intake rates could afford to invest sufficient time in being vigilant to affect their survival, or

that efficient foraging itself facilitates vigilance (Cresswell *et al.* 2003). Having a high intake rate may also allow an individual to forage in a larger flock, or to forage closer to conspecifics, where competition will be higher (Minderman *et al.* 2006) but risk will be reduced (Hamilton 1971; Cresswell 1994b; Quinn and Cresswell 2006).

Survival also varied between years. Risk of starvation during colder weather means that avoidance of predation risk by redshanks is not always possible (Cresswell 1994a; Yasué *et al.* 2003). The difference in survival between the two years may reflect this, with one winter being colder and with higher redshank density, so that more juvenile redshanks were forced to forage on the saltmarsh (see Cresswell and Whitfield 2008). In contrast, adults in our system are probably better able to cope with the lower energetic gains of non-saltmarsh habitats, even during colder weather. Adults are recorded rarely on the saltmarsh and suffer much lower overall winter mortality rates than juveniles (Cresswell 1994a). Adults could be more effective foragers than juveniles, or possibly have an increased ability to establish and defend a foraging territory in safer areas. It seems likely that differences in foraging efficiency between adults and juveniles might also be found within the population of juvenile redshanks. Variation in foraging ability on the mud flats, and so energy budget there, may then determine which redshanks have to spend time on the saltmarsh to meet their daily energy needs (see Yasué *et al.* 2003).

Overall, selection acts on the redshanks to avoid risk and to forage in a less profitable environment whenever possible, thus trading-off food with safety. When ecological conditions increase starvation risk and constrain individuals to feed in profitable but risky areas, individuals use vigilance to avoid capture and selection also then acts on this more specific anti-predation behaviour. In terms of individual mortality, vigilance can only ever partially mitigate predation risk, as vigilance does not guarantee successful evasion of capture. Consequently vigilance may have a relatively weaker effect on survival overall in our system. When avoidance is not costly to an individual, survival may be entirely determined by avoidance and not specific capture reducing anti-predation behaviours. However, when the cost of predator avoidance increases (for example increased starvation risk in cold weather) individuals must expose themselves to risk and survival is also determined by ability to mitigate the increased risk. Our limited evidence for between-year (and probably within-year)

variation in time exposed to risk may provide evidence for variation in the intensity and direction of selection on anti-predation behaviours, such as vigilance, so maintaining variation in them within the population. Perfect avoidance of predators is rarely achieved and environmental stochasticity also constrains avoidance, meaning selection will be periodically maintained on escape enhancing behaviours such as vigilance.

Studying behaviour and its consequences on individual fitness in natural systems is difficult to achieve (Lind and Cresswell 2005), which may explain why so few studies have investigated the effects of multiple behaviours on survival. However, in order to determine the relative importance of anti-predation behaviours ranging from general to specific, studies need to be conducted in the context of the entire system. When individuals are studied in natural systems where they can fully compensate for predation risk through a range of behaviours, the importance of very general, but often “invisible” predator avoidance behaviours on survival can be appreciated.

ACKNOWLEDGEMENTS

We thank John Quinn, Ross Macleod, Mark Hulme, Bobby Anderson, Emma and Alva Lind, Jeroen Minderman, East Lothian District Council, and the Tynninghame Estate for logistical help. We also thank the two anonymous referees whose comments helped substantially to improve a previous version of this article. AS was supported by a NERC studentship to WC, WC is a Royal Society University Research fellow, and JL was funded by the Swedish Research Council.

REFERENCES

- Abramsky, Z., Strauss, E., Kotler, B. P., Riggs, G., and Riechman, A. (1996). The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G.pyramidum*. *Oecologia* **105**, 313-319.
- Agrawal, A. A. (2001). Phenotypic plasticity in the interactions and evolution of species. *Science* **294**, 321-326.
- Altendorf, K. B., Laundre, J. W., Gonzalez, C. A. L., and Brown, J. S. (2001). Assessing effects of predation risk on the foraging behaviour of mule deer. *Journal of Mammalogy*. **82**, 430-439.
- Brodie, E. D. and Formanowicz, D. R. (1991). Predator avoidance and antipredator mechanisms - distinct pathways to survival. *Ethology Ecology & Evolution* **3**, 73-77.
- Brown, J. S. and Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters* **7**, 999-1014.
- Burton, N. H. K. (2000). Winter site-fidelity and survival of Redshank *Tringa totanus* at Cardiff, south Wales. *Bird Study* **47**, 102-112.
- Caro, T. M. (1995). Pursuit-deterrence revisited. *Trends in Ecology and Evolution* **10**, 500-503.
- Caro, T. M. (2005). 'Antipredator defenses in birds and mammals.' (University of Chicago Press: Chicago.)
- Cox, D. R. (1972). Regression models and life-tables. *Journal of the Royal Statistical Society* **34**, 187-220.
- Cresswell, W. (1994a). Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *Journal of Animal Ecology* **63**, 589-600.
- Cresswell, W. (1994b). Flocking is an effective anti-predation strategy in Redshanks, *Tringa totanus*. *Animal Behaviour* **47**, 433-442.

- Cresswell, W. (1995). Selection of avian prey by wintering sparrowhawks *Accipiter nisus* in southern Scotland. *Ardea* **83**, 381-389.
- Cresswell, W. (2008). Non-lethal effects of predation in birds. *Ibis* **150**, 3-17.
- Cresswell, W., Lind, J., Quinn, J. L., Minderman, J., and Whitfield, D. P. (2007). Ringing or colour-banding does not increase predation mortality in redshanks *Tringa totanus*. *Journal of Avian Biology* **38**, 309-316.
- Cresswell, W. and Quinn, J. L. (2004). Faced with a choice, predators select the most vulnerable group: implications for both predators and prey for monitoring relative vulnerability. *Oikos* **104**, 71-76.
- Cresswell, W., Quinn, J. L., Whittingham, M. J., and Butler, S. (2003). Good foragers can also be good at detecting predators. *Proceedings of the Royal Society of London Series B* **270**, 1069-1076.
- Cresswell, W. and Whitfield, D. P. (1994). The effects of raptor predation on wintering wader populations at the Tynninghame estuary, southeast Scotland. *Ibis* **136**, 223-232.
- Cresswell, W. and Whitfield, D. P. (2008). How starvation risk in Redshanks *Tringa totanus* results in predation mortality from Sparrowhawks *Accipiter nisus*. *Ibis* **150**, 209-218.
- Dill, L. M. (1990). Distance-to-cover and the escape decisions of an African cichlid fish, *Melanochromis chipokae*. *Environmental Biology of Fishes* **27**, 147-152.
- Durant, S. M. (2000). Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology* **11**, 624-632.
- Fraser, D. F., Gilliam, J. F., and Yip-Hoi, T. (1995). Predation and an agent of population fragmentation in a tropical watershed. *Ecology* **76**, 1461-1472.

- Gilliam, J. F. and Fraser, D. F. (1987). Habitat selection when foraging under predation hazard: a model and a test with stream-dwelling minnows. *Ecology* **68**, 1856-1862.
- Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology* **31**, 295-311.
- Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J., and Dill, L. M. (2009). Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *Journal of Animal Ecology* **78**, 556-562.
- Hilton, G. M., Cresswell, W., and Ruxton, G. D. (1999a). Intra-flock variation in the speed of response on attack by an avian predator. *Behavioral Ecology* **10**, 391-395.
- Hilton, G. M., Ruxton, G. D., and Cresswell, W. (1999b). Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. *Oikos* **87**, 295-302.
- Kaby, U. and Lind, J. (2003). What limits predator detection in blue tits (*Parus caeruleus*): posture, task or orientation? *Behavioral Ecology and Sociobiology* **54**, 534-538.
- Kohler, S. L. and McPeck, M. A. (1989). Predation risk and the foraging behaviour of competing steam insects. *Ecology* **70**, 1181-1825.
- Krams, I. A. (1996). Predation risk and shifts of foraging sites in mixed willow and crested tit flocks. *Journal of Avian Biology* **27**, 153-156.
- Lima, S. L. (1990). Protective cover and the use of space: different strategies in finches. *Oikos* **58**, 151-158.
- Lima, S. L. (1992). Strong preference for apparently dangerous habitats-a consequence of differential escape from predators. *Oikos* **64**, 597-600.

- Lima, S. L. (1998a). Nonlethal effects in the ecological effects of predator-prey interactions- What are the ecological effects of anti-predation decision making? *Bioscience* **48**, 25-34.
- Lima, S. L. (1998b). Stress and decision making under the risk of predation: recent developments from behavioural, reproductive and ecological perspectives. *Advances in the Study of Behaviour* **27**, 215-290.
- Lima, S. L. and Bednekoff, P. A. (1999). Back to basics of antipredatory vigilance: can nonvigilant animals detect attack? *Animal Behaviour* **58**, 537-543.
- Lima, S. L. and Dill, L. M. (1990). Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619-640.
- Lind, J. (2004). What determines probability of surviving predator attacks in bird migration?: the relative importance of vigilance and fuel load. *Journal of Theoretical Biology* **231**, 223-227.
- Lind, J. and Cresswell, W. (2005). Determining the fitness consequences of anti-predation behaviour. *Behavioral Ecology* **16**, 945-956.
- Mao, J. S., Boyce, M. S., Smith, D. W., Singer, F. J., Vales, D. J., Vore, J. M., and Merrill, E. H. (2005). Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Wildlife Management* **69**, 1691-1707.
- Minderman, J., Lind, J., and Cresswell, W. (2006). Behaviourally mediated indirect effects: interference competition increases predation mortality in foraging redshanks. *Journal of Animal Ecology* **75**, 713-723.
- Quinn, J. L. and Cresswell, W. (2004). Predator hunting behaviour and prey vulnerability. *Journal of Animal Ecology* **73**, 143-154.
- Quinn, J. L. and Cresswell, W. (2005). Escape response delays in wintering redshank, *Tringa totanus*, flocks: perceptual limits and economic decisions. *Animal Behaviour* **69**, 1285-1292.

- Quinn, J. L. and Cresswell, W. (2006). Testing for domains of danger in the selfish herd: sparrowhawks target widely spaced redshanks in flocks. *Proceedings of the Royal Society of London Series B* **273**, 2521-2526.
- Rochette, R. and Dill, L. M. (2000). Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. *Journal of Experimental Marine Biology and Ecology* **263**, 165-191.
- Sergio, F., Marchesi, L., and Pedrini, P. (2003). Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. *Journal of Animal Ecology* **72**, 232-245.
- Sih, A., Bell, A., and Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution* **19**, 372-378.
- Sparrevik, E. and Leonardsson, K. (1995). Effects of large *Saduria entomon* (Isopoda) on spatial distribution of their small *S. entomon* and *Monoporeia affinis* (Amphipoda) prey. *Oecologia* **101**, 177-184.
- Stuart-Smith, A. K. and Boutin, S. (1995). Behavioural differences between surviving and degraded juvenile red squirrels. *Ecoscience* **2**, 34-40.
- Todd, I. A. and Cowie, R. J. (1990). Measuring the risk of predation in an energy currency: field experiments with foraging blue tits *Parus caeruleus*. *Animal Behaviour* **40**, 112-117.
- Valeix, M., Loveridge, A. J., Chammille-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., and Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology* **90**, 23-30.
- Walther, B. A. and Gosler, A. G. (2001). The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (Aves: *Parus*). *Oecologia* **129**, 320.

Watson, M., Aebischer, N. J., and Cresswell, W. (2007). Vigilance and fitness in grey partridges *Perdix perdix* :the effects of group size and foraging-vigilance trade-offs on predation mortality. *Journal of Animal Ecology* **76**, 211-221.

Watts, B. D. (1991). Effects of predation risk on distribution within and between habitats in savannah sparrows. *Ecology* **72**, 1515-1519.

Werner, E. E. and Peacor, S. D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**, 1083-1100.

Whittingham, M. J., Stephens, P. A., Bradbury, R. B., and Freckleton, R. P. (2006). Why do we still you stepwise modelling in ecology and behaviour? *Journal of Animal Ecology* **75**, 1182-1189.

Wooster, D. and Sih, A. (1995). A review of the drift and activity responses of stream prey to predator presence. *Oikos* **73**, 3-8.

Yasué, M., Quinn, J. L., and Cresswell, W. (2003). Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in redshanks. *Functional Ecology* **17**, 727-736.

CHAPTER 4:

How is the distribution of redshanks (*Tringa totanus*) overwintering on the Fife coast related to habitat profitability, predation risk, starvation risk and population density? *



ABSTRACT

Foraging animals such as migratory shorebirds make decisions about where to spend the winter based on where they are most likely to avoid predation while still meeting their energy budget. But when temperatures are low and energy demands increase, individuals have a higher starvation risk and some may have to prioritise foraging over predation risk by moving to forage in more profitable but more risky locations. Movements could occur over the scale of a few kilometres with individuals moving to a new more profitable area, which poses a greater predation risk; or by moving only a few meters to a more risky location within a current foraging patch. We investigated potential movements of wintering redshanks on the east coast of Scotland in response to lower temperatures at two spatial scales. Firstly we determined if low temperatures caused redshanks to move a few kilometres into coastal areas that were more profitable, but posed a higher risk of predation. Secondly we investigated if low temperatures caused redshanks to move closer to predator concealing cover within their current foraging areas, and if such movements were dependant on habitat profitability. We also considered the effects of population density on distribution because high population densities may constrain movements between sites. We used distance from the shore to the mean low tide line as an index of actual and/or perceived predation risk. Habitat type was used as an indicator of profitability. We found no evidence for any effects of temperature on the distribution of redshanks either between or within areas and no evidence that cold weather caused redshanks to spatially trade-off foraging gains against risk. When the overall population was higher, more redshanks were counted on lower profitability rocky shore sites. This may be due to redshanks being ‘forced’ to overwinter on poorer foraging habitats when the population is higher, because they are excluded by competition with individuals that arrive earlier in the year and that fill up the highest quality foraging areas. The results suggest that redshanks are constrained in their ability to cope with lower habitat profitability by moving to other sites, and that any compensation for increased starvation risk is likely to occur through increased foraging effort in the same site, at the expense of behaviours that reduce predation risk.

*I collected 60% of the raw data. I carried out 100% of the analysis and 100% of the write-up with my collaborator commenting on and correcting earlier drafts.

INTRODUCTION

Most animals must meet their energy budget under risk of predation. This often leads to trade-offs between behaviours that maximise energy intake and those which minimise risk of predation (Lima and Dill 1990; Lima 1998b; Lind and Cresswell 2005). For overwintering shorebirds, these trade-offs affect many aspects of behaviour, for example, predation risk can be reduced by foraging in groups (Cresswell 1994b; Whitfield 2003b; Cresswell and Quinn 2004) and through increased vigilance (Hilton *et al.* 1999). However, this is often at a cost to intake rates, through increased competition (Goss-Custard and Le V. Dit Durell 1988; Minderman *et al.* 2006) or loss of time foraging because vigilance and scanning for food are often incompatible (Pulliam 1973; Watson *et al.* 2007).

Predation risk is also often traded-off against foraging gains spatially through choice of foraging location during the winter. This can be on the scale of a few meters or less, for example choice of foraging location within a group may decrease predation risk but also increase the effects of competition (Quinn and Cresswell 2006); on an intermediate scales, with individuals balancing their distance from predator concealing cover with foraging gains (Pomeroy 2006; Whitfield 2003b) or on larger spatial scales, for example by choosing a site on which to forage in relation to risk and foraging attributes (Pomeroy *et al.* 2008). Individuals often choose to forage in locations where predation risk is lower, even if this is at a cost to intake rates (Cresswell 1994a; Yasué *et al.* 2003; Pomeroy 2006).

During cold weather individuals may not be able to balance risk and intake so effectively and may have to increase their risk of predation to meet their increased energy demands (Pomeroy *et al.* 2008; Yasué *et al.* 2003). This may be achieved by moving to forage in locations that are more profitable, but also more risky. Such movements can also occur on a variety of spatial scales. On a small scale, within habitats, for example, with individuals moving to profitable patches a few meters closer to predator concealing cover (Whitfield 2003b). On intermediate scales, with individuals choosing more risky habitat within a few hundred of meters (Cresswell 1994a; Cresswell and Whitfield 2008; Yasué *et al.* 2003); and on a larger scale, with individuals sometimes moving kilometres to new sites (Evans 1976).

When considering decisions about overwintering locations and movements between sites it is important to consider overall population size. This is because site choice and movements between sites may be constrained by population density effects (Goss-Custard *et al.* 1996). When population density is low and far from carrying capacity, then only ‘optimal’ sites will be occupied (i.e. profitable safe sites) (Charnov 1976; Moody *et al.* 1996). In this case there will be no apparent effect of cold weather on distribution as these sites provide the best foraging option in all conditions. However, if decreasing temperature reduces the carrying capacity of the occupied sites below that of the population or if additional individuals enter a population where optimal foraging sites are already at carrying capacity this may force some individuals to occupy lower quality sites due to increased competition for the best foraging locations (Gill *et al.* 2001; Sutherland and Parker 1985; Fretwell and Lucas 1970). If populations reach carrying capacity across all habitats, then there may be little flexibility for redistribution in colder weather, and there will also be strong competition for the best foraging sites (Goss-Custard 1985).

We studied the site use of redshanks (*Tringa totanus*) overwintering on the east coast of Scotland, using a variety of different habitats, which varied in profitability. We investigated the way in which redshanks responded to increased energy demands (caused by cold weather) with respect to predation risk and profitability. Redshanks have previously been shown to respond to changes in energy demands within a winter, by moving to profitable but risky areas (Cresswell 1994a; Yasué *et al.* 2003). We measured the effect of temperature on the distribution of redshanks on two spatial scales.

Firstly, we looked for movements of redshanks between sites, investigating the way in which temperature affected the number of redshanks foraging on different habitat types and if individuals traded off foraging gains with predation risk. We specifically predicted that redshank numbers should change with lower temperatures, depending on profitability and risk, as follows:

1. Numbers in profitable but safe areas should be highest and remain stable with temperature, because this is always the best foraging option in terms of risk and foraging gains.

2. Numbers in profitable but risky areas should increase during cold weather, because these should only be used when energy budgets cannot be met in safer areas.
3. Numbers in less profitable but safe areas should decrease with cold weather, when individuals cannot meet their energy budgets.
4. Numbers in less profitable but risky areas should always be low and remain stable with temperature, because these are always the worst foraging option in terms of risk and foraging gains, unless population size increases (see below).

We also considered the way in which temperature affected movements of redshanks within sites, with respect to predation risk and habitat type. In habitats consisting of open bays or harbours where large amounts of seaweed accumulate at the high-tide line a profitable foraging habitat exists which is, however, close to predator concealing cover. If individuals can use this resource to increase their intake rate at a cost of increasing their predation we predict that:

1. When temperatures are lower, redshanks on harbour and bay habitats should move closer to cover in order to meet their energy budgets as seaweed washed up provides a highly profitable foraging option.
2. Temperature should not affect foraging location of redshanks on rocky habitats, because the lack of large amounts of washed up sea weed on this habitat means there is no foraging gain from feeding closer to cover under increased predation risk (in fact seaweed and available prey are likely to increase further from the shoreline).

We also investigated whether the total population size had any effect on the relative distribution of redshanks across sites and predict that:

1. When population size is lower during the winter, then counts should be lower on more risky and less profitable sites.
2. When the population is higher during the winter, counts may increase on high risk and less profitable sites, because redshanks are more constrained in their choice of sites through intraspecific competition.

METHODS

Study system

The Fife coast is on the east of Scotland to the north of the Firth of Forth and south of the Tay estuary. The coast is made up of a variety of habitat types but is dominated by areas of rocky and often complex shoreline. This is interspersed large sandy bays and also contains muddy harbour areas located in conjunction with towns and villages.

Redshanks overwinter across all these different habitat types. The section of coast from immediately to the east of St-Andrews and up to and including St-Monans was covered by this study (see Figure 4.1).

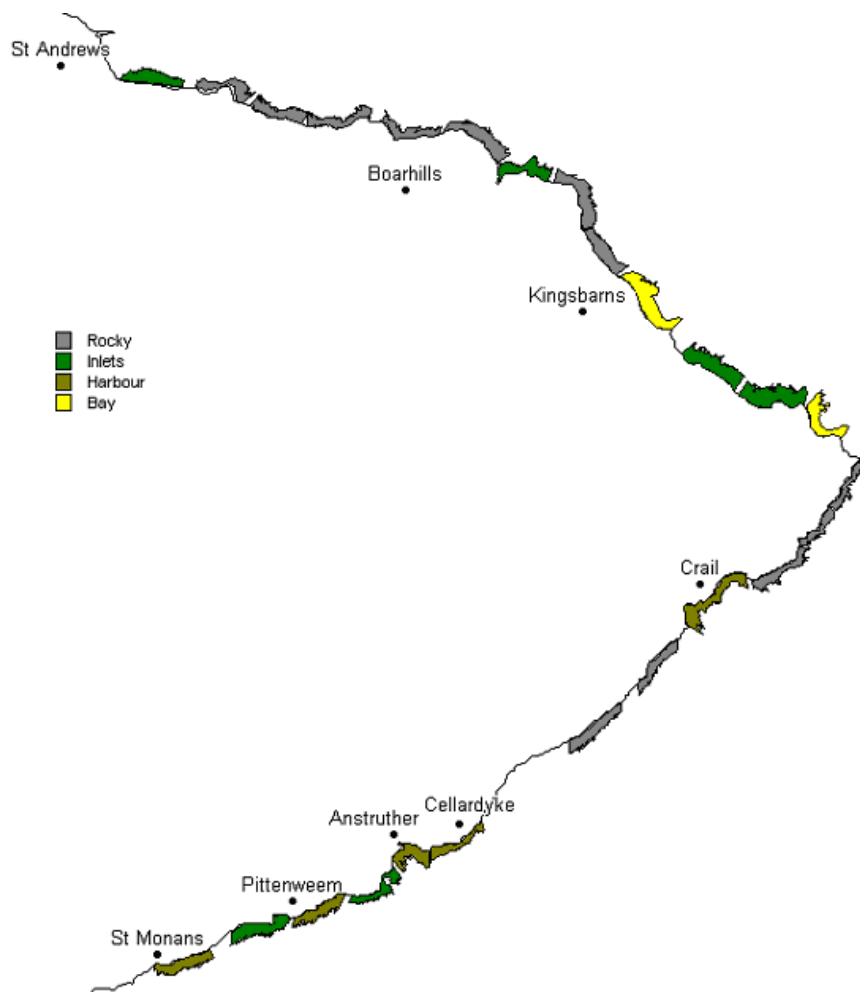


Figure 4.1. Map of the section of the coast of Fife counted, with villages and towns labelled; locations of the 25 count sectors are shown with differing colours to represent the four major habitat types within each sector: (i) rocky shore, (ii) rocky areas dominated by inlets, (iii) sandy bays or (iv) a sector containing one or more harbour. A section of coast between Crail and Cellardyke was excluded from analysis because this contained a pig farm on which redshanks were regularly seen to forage.

This area was probably not representative of the foraging risk trade-offs redshanks might have made along the rest of the coastal area counted and also was difficult to assess in terms of the way in which site-use would have affected predation risk. Small 'gaps' between sectors are artefacts of fitting sectors to coincide with harbours and maintain sectors of approximately even length.

Measuring site use by redshanks

Redshanks were counted on four occasions during the winter of 2006/07 in October, December, February and March. All counts were made within an hour and a half of low tide and were conducted from the shore by scanning the intertidal area for redshanks using binoculars or a telescope. Each redshank's position was logged from the shore using a hand-held GPS; additionally the distance of each redshank from the shore was estimated to the nearest 10m. The coastal area counted was then divided into 25, 1km (approximately) sectors (Figure 4.1). From the count data and spatial information for the position of each redshank, the total number of redshanks counted within each sector could be calculated for each survey.

Index of predation risk

Sparrowhawks (*Accipiter nisus*), and other raptors, which prey on redshanks, are more likely to be successful when they attack from concealing cover (Cresswell 1996; Whitfield 1985; Whitfield 2003b); more open areas far from cover may also increase redshanks ability to detect predators such as peregrine falcons (*Falco peregrinus*). Therefore the further from cover that a redshank can forage, the lower its risk of predation. Raptor concealing cover occurs predominantly at the shoreline of coastal sites. This means sites with more habitat available far from cover (i.e. sites with a large distance from the shore to the water) should have, or be perceived by redshanks to have, a lower risk of predation (Cresswell 2008; Lima 1998a; Pomeroy *et al.* 2008). Within sites, the further redshanks choose to forage from predator concealing cover at the shore should also affect its risk of predation by reducing the chance of a successful attack (Pomeroy *et al.* 2006; Whitfield 2003b).

Habitats and profitability

The intertidal habitats of count sectors were broadly classified into one of four categories: (i) rocky shore - areas of rocky shore with no (or few) inlets, characterised by bare rock, with seaweed growing on rocks and pools, (ii) rocky inlets - areas of

rocky shore where rocks are interspersed with small inlets of muddy sand, sand and shingle, (iii) sandy bays - areas mainly consisting of a large sandy beach or (iv) muddy harbours- sectors containing one or more (Figure 4.1). Mud is likely to be a food rich environment providing a profitable foraging substrate for redshanks. This is reflected in the redshanks preference to overwinter in muddy areas (Hill *et al.* 1993), and in the dietary preferences of redshanks, which tends towards prey species found in muddy substrates such as *Corophium sp.* (Goss-Custard 1969). Muddy harbours often had large mats of seaweed containing *Orchestia sp.* and other invertebrate prey. Therefore areas containing a muddy harbour should be most profitable to redshanks. Sandy areas also had large mats of washed-up seaweed often containing large numbers of *Orchestia sp.* Redshanks were also observed foraging successfully by probing into soft wet sand at the waters edge; therefore sandy areas probably represent the next most profitable foraging option for redshanks both in terms of number of prey available and in terms of redshank's ability to obtain prey. Rocky areas sometimes contained little or no food for redshanks (in the case of bare rock) and foraging on seaweed covered rock or in pools was likely to provide the least profitable foraging environment in terms of prey available and redshank foraging ability on this substrate (Cresswell 1994a; Yasué *et al.* 2003; Goss-Custard 1969). Rocky areas with many inlets were a mixture of sandy and rocky habitats and therefore probably provide an intermediate foraging environment between sandy bays and rocky shores- in terms of profitability. However, it should be noted that for the purposes of testing our hypotheses we only need *differences* in habitat profitability, not an exact identification of which habitats are the most profitable.

Measuring sector characteristics

Ordnance survey maps of the Fife coast, at the scale of 1:25000, were used in order to establish the profitability and perceived and/or actual predation risk at each count sector. The main habitat of sectors was estimated directly from the maps. The mean distance from the shoreline to the mean low tide line was calculated from the mean of four measurements of this distance, evenly spaced along each sector. These measurements were made in MapInfo (version 6.0) using a digitised ordnance survey map. The area of each sector was measured in MapInfo by drawing a polygon for each sector using the ordnance survey map as a template.

Weather data

Weather data was collected from Vantage ProTM weather stations (Davis Instruments, Hayward, California, USA) at St-Andrews (from October to February) and Crail (in March) Figure 4.1. We investigated the effects of temperature on distribution on a closely matched time scale by calculating the mean minimum temperature over three days- two days before and the day of the survey.

Model Parameters

We simplified the names of some of our model variables for clarity, as follows:

Distance Risk=Mean distance from the shoreline to the mean low tide line at each sector.

Profitability=Determined by habitat type of a sector, we classified different habitats as follows (from most to least profitable): Harbour (area containing a harbour), Sandy bay (area dominated by sandy beach), Inlets (rocky shore with many inlets), Rocky Shore (rocky areas without inlets).

Total Count=Total count from all sectors (i.e. an index of population density at the time of each survey). Counts were made during late autumn and early spring, therefore we expect some variation in population size due to migration to and from overwintering and breeding sites.

Within Sector Risk= For each count the mean distance from cover of a sector minus the mean estimated distance from the shore for redshanks counted in that sector. This was modelled as a dependant variable (see below), as an index of the mean distance at which birds were actually seen foraging during each survey, to investigate any temperature dependent movement within each sector. By using this measure we controlled for any constraints redshanks are under, in terms of actual distance from the shore available (e.g. the distance at low tide from the high tide line to the sea varied across sites).

Other variables modelled were the sector the count was made in and the area of each sector. Minimum temperature was considered within 3 days of each count (including the day of the count).

Analysis

The effects of temperature, risk and profitability on distribution were modelled using generalised estimating equations (GEEs). Analyses were conducted using SAS (version 9.2). ‘Count sector’ was included as the repeated variable to account for the fact that repeated counts were made in the same sectors for each survey; we used an exchangeable correlation structure (i.e. all counts within sectors are equally likely to be correlated with one another). Log of site area was used as an offset to account for ‘effort’ effects (i.e. more birds are likely to be counted in larger areas). The count data were overdispersed; therefore a scaling factor was also included in all models. Models for movement between sectors used ‘count’ as the dependant variable and used a Poisson distribution. To test for any movement within sectors that was dependant on temperature and/or habitat we used a GEE (as described above) to model ‘Within Sector Risk’ as the dependant variable with a normal distribution. Models testing for population size effects on distribution, between sectors, again used ‘count’ as the dependant variable with a Poisson distribution.

We wanted to investigate which models provided the best fit for our data, but also which would provide us with the most ‘biologically meaningful’ test of our hypotheses. To do this we investigated the significance of all model parameters using the type III, chi-squared analysis for the ‘full’ GEE models (i.e. with all parameters in the model). We then removed non-significant variables one parameter at a time. For the full model and every subsequent model we calculated the QICu value. This is a measurement for goodness of fit similar to Akaike’s information criterion but for quasi-likelihood modelling methods, where a lower QICu value indicates a better fit to the data (Hardin and Hible 2003; Pan 2001). For each step the significance of each parameter was reassessed. Model selection continued until all variables that were non-significant or not close to significance were removed; or until further model reduction greatly increased the QICu value of the model. Models were sorted in ascending order of QICu and the change in QICu comparing the ‘top’ model (i.e. the model with the lowest QICu) to all others was calculated. Models that differed from the ‘top’ model

in QICu by less than 4, were considered to be reasonably equivalent in terms of goodness of fit (Burnham and Anderson 2002). Once a model had been selected its biological implications were further investigated by consideration of its parameter estimates.

RESULTS

Effects of temperature on distribution between sectors

The mean minimum temperature (in degrees Celsius) for survey days varied between counts as follows (standard errors in brackets): October 8.42 (+/-0.5); December 3.19 (+/-0.34); February 6.16(+/-0.28); March 3.44 (+/-0.11).

We found no significant interactions in redshank site usage with temperature and predation risk (in terms of distance from the shore) or profitability (Table 4.1). This suggests that redshanks did not move between sectors during cold weather in order to meet their energy demands, nor was there any trade-off between foraging gains and increased predation risk. None of the two-way interactions were subsequently found to be significant on removal of the three-way interactions (or other non-significant two-way interactions). Therefore no model selection was conducted.

Table 4.1. Type III analysis for a generalised estimating equation investigating the effect of temperature on numbers of redshanks counted in each sector in relation to predation risk and profitability of count sectors.

Model Parameter	d.f	Chi-Square	P
Total Count	1	2.07	0.1499
Profitability	3	3.9	0.2726
Distance Risk	1	1.98	0.1596
Minimum Temperature	1	0.94	0.3335
Distance Risk*Profitability	3	3.74	0.2908
Distance Risk*Minimum Temperature	1	1.94	0.1634
Minimum Temperature*Profitability	3	3.91	0.2709
Distance Risk*Minimum Temperature*Profitability	3	3.85	0.2784

Effects of temperature on distribution within sectors

When we modelled ‘Within Sector Risk’- the mean distance of redshanks from cover in relation to overall risk within sectors, we found no evidence that redshanks moved within sectors. Redshank foraging distance from cover was not affected by which habitat type they foraged in and positions with respect to predation risk did not change with temperature. Nor was there any evidence that individuals in different habitats altered their exposure to predation risk in different ways in response to cold weather (Table 4.2). Removal of the non-significant two-way interaction did not result in any significant main effects. No model selection or further investigation way carried out.

Table 4.2. Type III analysis for a generalised estimating equating investigating the effect of temperature on redshank distance from cover within count sectors, , and how this is affected by habitat type.

Model parameter	d.f.	Chi-Square	P
Profitability	3	5.86	0.1185
Total Count	1	0.7	0.4038
Minimum Temperature	1	2.75	0.0971
Minimum Temperature*Profitability	3	4.97	0.1737

Population density effects on distribution

We found evidence that distribution of redshanks between sectors was dependent on overall population size, with a significant interaction between count size and profitability (Table 4.3). Removal of the non-significant interaction terms from the model did not improve the model fit (Table 4.4); therefore we used the full model to further explore this effect using the model parameter estimates (Table 4.5).

Table 4.3. Type III analysis for a generalised estimating equating investigating the effect of population density on the numbers of redshanks counted in each sector in relation to temperature, the predation risk and profitability of count sectors. Significant P values are marked in bold.

Model Parameter	d.f.	Chi-Square	P
Total Count	1	0.75	0.385
Distance Risk	1	0.2	0.6545
Profitability	3	10.47	0.0149
Minimum Temperature	1	0.1	0.7575
Total Count*Profitability	3	10.12	0.0176
Total Count*Distance Risk	1	0.01	0.9291
Total Count*Minimum Temperature	1	0.14	0.7068

Table 4.4. Testing the goodness of fit of models as non-significant model parameters were removed. Models are ordered by descending QICu, with the model providing the ‘best’ fit to the data appearing first.

Model	QICu	Change in QICu
Total Count + Profitability + Distance Risk + Minimum Temperature + Profitability*Total count + Distance Risk*Total count + Minimum Temperature*Total Count	-617.19	0
Total count + Profitability + Distance Risk + Minimum Temperature + Profitability*Total Count	-610.17	7.02
Total count + Profitability + Distance Risk + Minimum Temperature + Profitability*Total count + Distance Risk*Total Count	-601.23	15.96

We found no evidence that overall population density affected where redshanks foraged in relation to predation risk, or that population density effects depended on temperature because there were no significant interactions between total count and risk or temperature (Tables 4.3 and 4.5). The total number of Redshanks counted on each survey varied and a significant interaction between count size and profitability indicates that the change in numbers with population size was dependent on habitat

type. Figure 4.2 and the parameter estimates in Table 4.5 show that when more redshanks were present overall, the number of individuals counted on the least profitable (rocky shore) areas increased but counts on other habitat types did not vary with overall count size. Figure 4.2 also shows that fewer birds were using the less profitable rocky shore habitat compared to other more profitable habitats.

Table 4.5. Parameter estimates for the generalised estimating equation investigating population density effects. Significant terms a marked in bold.

Model parameter	Factor level	Estimate	Standard error
Intercept		3.93	2.473
Total Count		0.006	0.01
Distance Risk		-0.005	0.01
Profitability	Harbour	1.82	1.187
Profitability	Inlets	0.359	0.963
Profitability	Rocky shore	-5.704	1.531
Profitability	Sandy bay	0	0
Minimum Temperature		0.114	0.32
Total Count*Profitability	Harbour	-0.006	0.005
Total Count*Profitability	Inlets	-0.004	0.004
Total Count*Profitability	Rocky shore	0.011	0.006
Total Count*Profitability	Sandy bay	0	0
Total Count*Distance Risk		0	0
Total Count*Minimum Temperature		-0.001	0.001

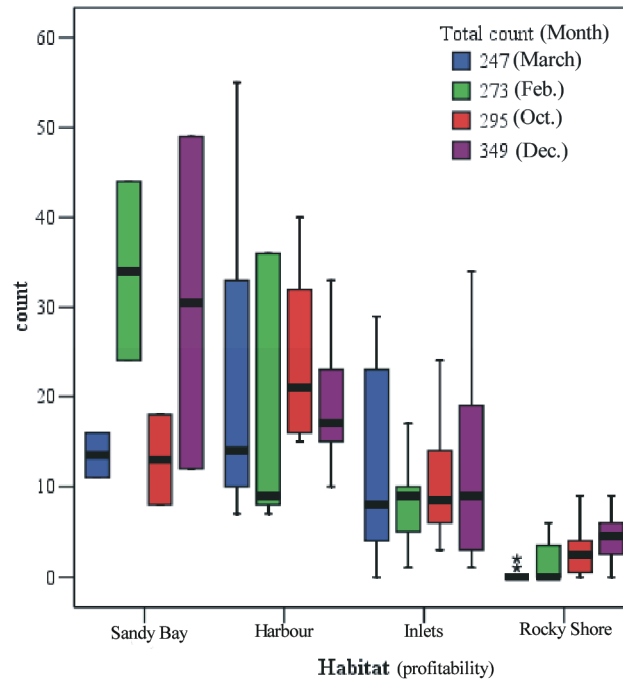


Figure 4.2. Box-plot showing that the number of redshanks counted on rocky areas increased with increased population density (increased total count). Other habitat types showed no clear pattern of change with overall count size. * Indicates an outlier.

DISCUSSION

The redshanks overwintering in the areas covered by this study did not move between different coastal habitats depending on changes in temperature. Individuals did not appear to trade-off foraging gains against predation risk by moving to forage in more profitable, but riskier sites. That we do not observe this predicted trade-off might be because over the course of the winter covered by this study the temperature was never low enough, or there was not enough variation in temperature to force individuals to alter their foraging location with respect to profitability or risk. Our study covered a typical recent “mild” UK winter (there were few days below freezing, and most days were above 5 degrees C), where starvation risk for wintering redshanks may be relatively low. Even if temperatures are variable, as long as they remain over the threshold necessary for an individual redshank to meet its daily energy needs, then they will probably not affect site choice decisions (Yasué *et al.* 2003). It may also be that the most profitable and safe sites had the capacity for large numbers of overwintering redshanks. Individuals in these areas would not need to move in response to changes in temperature because such sites provide an optimal foraging location in terms of balancing risk with energy intake. However we also found no

variation in site usage with predation risk, even when temperatures were higher. It may be that there was not a large disparity in risk of predation between ‘high’ and ‘low’ risk sites (in terms of variation in distance from the shore to low tide).

If risk only varied moderately then it is possible that redshanks traded-off foraging gains with predation risk in ways other than by moving between sectors. Redshanks can compensate for predation risk in a number of ways that reduce the risk of capture, rather than behaviours that reduce the risk of attack (Lind and Cresswell 2005).

Within a site individuals could reduce risk, for example, by spending less foraging in order to spend more time being vigilant, which would decrease risk of capture (Arenz and Leger 2000; Bachman 1993; Fitzgibbon 1989) or by foraging in larger groups, which could decrease intake but should decrease predation risk (Beauchamp 2003). Behavioural compensation for risk such as this might be especially feasible if a site is highly profitable and although avoidance behaviours are likely to be most important in promoting survival (see Sansom *et al.* 2009), if attack rates are low at a site, and escape behaviours effective, then avoidance may not be necessary, (Lima 1992; Heithaus *et al.* 2009). Risk of attack may also be uniform because flexible and mobile predators such as sparrowhawks and particularly peregrines may respond to any redistribution of redshanks with movements of their own (Lima 2002; Cresswell 2008).

We also found that redshanks did not increase their predation risk by moving closer to cover within sites during colder weather. Within sectors individuals may not have been able to significantly increase their energy intake by moving closer to cover, meaning there was not a sufficient ‘pay-off’ to increasing their risk of predation (Brown and Kotler 2004); alternatively it may simply be that individuals across all habitats could meet their energy budgets at locations far from predator concealing cover in all temperatures, during our counts. Risk within sites could have varied in other ways, which we did not measure; for example, in areas of rocky shore areas and in small inlets, the topography of the shoreline may have meant that the least risky foraging location was not always far from the shoreline, given that rocky outcrops may also be used as cover for predators.

We did find, however, an effect of population density on distribution across habitats. The effects of such variation in population density on the distribution of redshanks can give us an insight into the way in which temperature related movements might be constrained by carrying capacity and intraspecific competition (Goss-Custard *et al.* 1996). When the population increased, during the middle of the winter, increased numbers of redshanks used rocky shore areas. However, we found no effect of population size on distribution in relation to risk, or any change in distribution in relation to population size that was dependant on temperature. This suggests that changes in the numbers of redshanks we counted were not related to changes in temperature and also confirms that redshanks are likely to be responding to variation in risk via behavioural compensation rather than showing a preference to distribute themselves away from the risky areas.

Overall redshanks appeared to show a preference for non-rocky shore habitats across all temperatures and population sizes. This suggests that redshanks were distributing themselves according to profitability, when possible, with more individuals using habitats that provided optimal foraging conditions (in terms of intake) (Charnov 1976). It is likely that increasing competition for more profitable foraging areas, when the population was larger, caused additional redshanks joining the population mid-winter to choose rocky sites, which although were less profitable, had fewer conspecifics competing for the food there (Milinski 1982; Goss-Custard 1980). This evidence for competition in profitable areas suggests that redshanks may to some extent be constrained by population density when choosing overwintering sites. If there is a strong preference for the most profitable sites, these may be ‘filled’ first regardless of risk, and so no temperature related movements into profitable risky sites were observed during colder weather. When the more profitable areas reach carrying capacity some individuals are likely to be forced to use the less preferred habitats (Gill *et al.* 2001). It may be that these individuals are those that arrived later in the winter, and so do not have an established foraging territory (Fretwell and Lucas 1970). Additionally variation in individual behaviour means that some individuals are likely to have a lower competitive ability (Caldow *et al.* 1999) and so may become displaced when population densities are higher and competition increases in the most popular foraging areas. There may also be an age-related effect of population density; if juvenile redshanks are less competitive than adults, or less able to defend a territory

they may be more likely than adults to be displaced by intense competition for the most preferred foraging habitat (Cresswell 1994a; Goss-Custard and Le V. Dit Durell 1987).

Overwintering in a less profitable area is likely to have knock-on effects on individual fitness. During colder weather individuals in less profitable foraging habitats will have an increased risk of starvation. This could be compensated for through behaviour, for example by spending less time on vigilance in order to spend more time foraging (Arenz and Leger 2000; Bachman 1993); however this will increase predation risk (Fitzgibbon 1989; Lima 1994). In this way population density effects may cause some individuals to trade-off foraging gains with predation risk, leading to increased predation mortality in colder winters if populations are high (Whitfield 2003a; Cresswell and Whitfield 2008). Overwintering in areas where intake rates are relatively lower may also affect body condition and time of migration to breeding grounds (Gill *et al.* 2001; Norris and Marra 2007). Individuals with that arrive later to breeding grounds or are in poor condition are less likely to occupy high quality breeding territories; attract mates in good condition and are likely to have a lower breeding success (Sandberg and Moore 1996; Kokko 1999).

Overall, we found no evidence that redshanks overwintering on coastal areas altered their foraging location in response to variation in temperature or predation risk over the course of the winter. It appears that redshanks responded to changes in their energy budget and to variation in risk via behavioural mechanisms or possibly by altering their foraging positions on a smaller scale than that at which we measured. This finding is consistent with previous studies of overwintering redshanks which have found them to be site-faithful (Burton 2000) and have relatively small foraging ranges (Burton and Armitage 2005). We did however find evidence that there is competition amongst individual redshanks for profitable foraging areas, and they only use poorer habitats more when population density is high. Overall this suggests that redshanks are vulnerable to reduction in habitat profitability or reduction in habitat area because they are unlikely to be preadapted and free to move to new sites, instead they appear to adapt to changes in local conditions by altering their behaviour rather than moving large distances to find a more favourable environment (Burton *et al.* 2006).

REFERENCES

- Arenz, C. L. and Leger, D. W. (2000). Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. *Animal Behaviour* **59**, 535-541.
- Bachman, G. (1993). The effect of body condition on the trade-off between vigilance and foraging in Beldings ground squirrels. *Animal Behaviour* **46**, 233-244.
- Beauchamp, G. (2003). Group-size effects in vigilance: a search for mechanisms. *Behavioural Processes* **63**, 111-121.
- Brown, J. S. and Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters* **7**, 999-1014.
- Burnham, K. P. and Anderson, D. R. (2002). 'Model selection and multimodel inference: A practical information-theoretic approach.' (Springer: New York.)
- Burton, N. H. K. (2000). Winter site-fidelity and survival of Redshank *Tringa totanus* at Cardiff, south Wales. *Bird Study* **47**, 102-112.
- Burton, N. H. K. and Armitage, M. J. S. (2005). Differences in the diurnal and nocturnal use of intertidal feeding grounds by Redshank *Tringa totanus*. *Bird Study* **52**, 120-128.
- Burton, N. H. K., Rehfish, M. M., Clark, N. A., and Dodd, S. G. (2006). Impacts of sudden winter habitat loss on the body condition and survival of redshank *Tringa totanus*. *Journal of Applied Ecology* **43**, 464-473.
- Caldow, R. W. G., Goss-Custard, J. D., Stillman, R. A., Le V.Dit Durell, S. E. A., Swinfen, R., and Bregnballe, T. (1999). Individual variation in the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and susceptibility to interference. *Journal of Animal Ecology* **68**, 869-878.
- Charnov, E. L. (1976). Optimal foraging and the marginal value theorem. *Theoretical Population Biology* **9**, 129-136.

- Cresswell, W. (1994a). Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *Journal of Animal Ecology* **63**, 589-600.
- Cresswell, W. (1994b). Flocking is an effective anti-predation strategy in Redshanks, *Tringa totanus*. *Animal Behaviour* **47**, 433-442.
- Cresswell, W. (1996). Surprise as a winter hunting strategy in Sparrowhawks *Accipiter nisus*, Peregrines *Falco peregrinus* and Merlins *F. columbarius*. *Ibis* **138**, 684-692.
- Cresswell, W. (2008). Non-lethal effects of predation in birds. *Ibis* **150**, 3-17.
- Cresswell, W. and Quinn, J. L. (2004). Faced with a choice, predators select the most vulnerable group: implications for both predators and prey for monitoring relative vulnerability. *Oikos* **104**, 71-76.
- Cresswell, W. and Whitfield, D. P. (2008). How starvation risk in Redshanks *Tringa totanus* results in predation mortality from Sparrowhawks *Accipiter nisus*. *Ibis* **150**, 209-218.
- Evans, P. R. (1976). Energy balance and optimal feeding strategies in waders: some implications for their distribution and movements in the non-breeding season. *Ardea* **64**, 117-139.
- Fitzgibbon, C. D. (1989). A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Animal Behaviour* **37**, 508-510.
- Fretwell, S. D. and Lucas, H. L. (1970). On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16-36.
- Gill, J. A., Norris, K., Potts, P. M., Gunnarsson, T. G., Atkinson, P. W., and Sutherland, W. J. (2001). The buffer effect and large-scale population regulation in migratory birds. *Nature* **412**, 436-438.

- Goss-Custard, J. D. (1969). The winter feeding ecology of the redshank *Tringa totanus*. *Ibis* **111**, 338-356.
- Goss-Custard, J. D. (1980). Competition for food and interference among waders. *Ardea* **68**, 31-52.
- Goss-Custard, J. D. (1985). Foraging behaviour of wading birds and the carrying capacity of estuaries. In 'Behavioural Ecology: Ecological Consequences of Adaptive Behaviour.' (Eds R. M. Sibly and R. H. Smith.) pp. 169-188. (Blackwell Scientific Publications: Oxford.)
- Goss-Custard, J. D. and Le V.Dit Durell, S. E. A. (1987). Age-related effects in oystercatchers, *Haematopus ostralegus*, feeding on mussels *Mytilus edulis*. III. The effect of interference on overall intake rate. *Journal of Animal Ecology* **56**, 549-558.
- Goss-Custard, J. D. and Le V.Dit Durell, S. E. A. (1988). The effect of dominance and feeding method on the intake rates of oystercatchers, *Haematopus ostralegus*, feeding on mussels. *Journal of Animal Ecology* **57**, 827-844.
- Goss-Custard, J. D., West, A. D., Clarke, R. T., and Le V.Dit Durell, S. E. A. (1996). The carrying capacity of coastal habitats for oystercatchers. In 'The Oystercatcher: from individuals to populations.' (Ed J. D. Goss-Custard.) pp. 327-351. (Oxford University Press: Oxford.)
- Hardin, J. W. and Hible, I. (2003). 'Generalized Estimating Equations.' (Chapman and Hall/ CRC)
- Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J., and Dill, L. M. (2009). Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *Journal of Animal Ecology* **78**, 556-562.
- Hill, D., Rushton, S. P., Clark, N., Green, P., and Prys-Jones, R. (1993). Shorebird communities on British estuaries: factors affecting community composition. *Journal of Applied Ecology* **30**, 220-234.

Hilton, G. M., Cresswell, W., and Ruxton, G. D. (1999). Intra-flock variation in the speed of response on attack by an avian predator. *Behavioral Ecology* **10**, 391-395.

Kokko, H. (1999). Competition for Early Arrival in Migratory Birds. *Journal of Animal Ecology* **69**, 940-950.

Lima, S. L. (1992). Strong preference for apparently dangerous habitats-a consequence of differential escape from predators. *Oikos* **64**, 597-600.

Lima, S. L. (1994). On the personal benefits of anti-predatory vigilance. *Animal Behaviour* **48**, 734-736.

Lima, S. L. (1998a). Nonlethal effects in the ecological effects of predator-prey interactions- What are the ecological effects of anti-predation decision making? *Bioscience* **48**, 25-34.

Lima, S. L. (1998b). Stress and decision making under the risk of predation: recent developments from behavioural, reproductive and ecological perspectives. *Advances in the Study of Behaviour* **27**, 215-290.

Lima, S. L. (2002). Putting predators back into behavioral predator-prey interactions. *Trends in Ecology and Evolution* **17**, 70-75.

Lima, S. L. and Dill, L. M. (1990). Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619-640.

Lind, J. and Cresswell, W. (2005). Determining the fitness consequences of anti-predation behaviour. *Behavioral Ecology* **16**, 945-956.

Milinski, M. (1982). Optimal foraging: the influence of intraspecific competition on diet selection. *Behavioural Ecology and Sociobiology* **11**, 109-115.

Minderman, J., Lind, J., and Cresswell, W. (2006). Behaviourally mediated indirect effects: interference competition increases predation mortality in foraging redshanks. *Journal of Animal Ecology* **75**, 713-723.

- Moody, A. L., Houston, A. I., and McNamara, J. M. (1996). Ideal free distributions under predation risk. *Behavioural Ecology and Sociobiology* **38**, 131-143.
- Norris, K. and Marra, P. P. (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor* **109**, 535-547.
- Pan, W. (2001). Akaike's Information Criterion in Generalized Estimating Equations. *Biometrics* **57**, 120-125.
- Pomeroy, A. C. (2006). Tradeoffs between food abundance and predation danger in spatial usage of stopover site by western sandpipers, *Calidris mauri*. *Oikos* **112**, 629-637.
- Pomeroy, A. C., Acevedo Seaman, D. A., Butler, R. W., Elner, R. W., Williams, T. D., and Ydenberg, R. C. (2008). Feeding-Danger Trade-Offs Underlie Stopover Site Selection by Migrants. *Avian Conservation and Ecology* **3**, 7.
- Pomeroy, A. C., Butler, R. W., and Ydenberg, R. (2006). Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger. *Behavioral Ecology* **17**, 1041-1045.
- Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology* **38**, 419-422.
- Quinn, J. L. and Cresswell, W. (2006). Testing for domains of danger in the selfish herd: sparrowhawks target widely spaced redshanks in flocks. *Proceedings of the Royal Society of London Series B* **273**, 2521-2526.
- Sandberg, R. and Moore, F. R. (1996). Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. *Oikos* **77**, 577-581.
- Sansom, A., Lind, J., and Cresswell, W. (2009). Individual behavior and survival: the roles of predator avoidance, foraging success and vigilance. *Behavioral Ecology* **In Press**.

Sutherland, W. J. and Parker, G. A. (1985). Distribution of unequal competitors. In 'Behavioural Ecology.' (Eds R. M. Sibly and R. H. Smith.) pp. 255-273. (Blackwell Scientific Publications: Oxford.)

Watson, M., Aebischer, N. J., and Cresswell, W. (2007). Vigilance and fitness in grey partridges *Perdix perdix* :the effects of group size and foraging-vigilance trade-offs on predation mortality. *Journal of Animal Ecology* **76**, 211-221.

Whitfield, D. P. (1985). Raptor predation on wintering waders in southeast Scotland. *Ibis* **127**, 544-548.

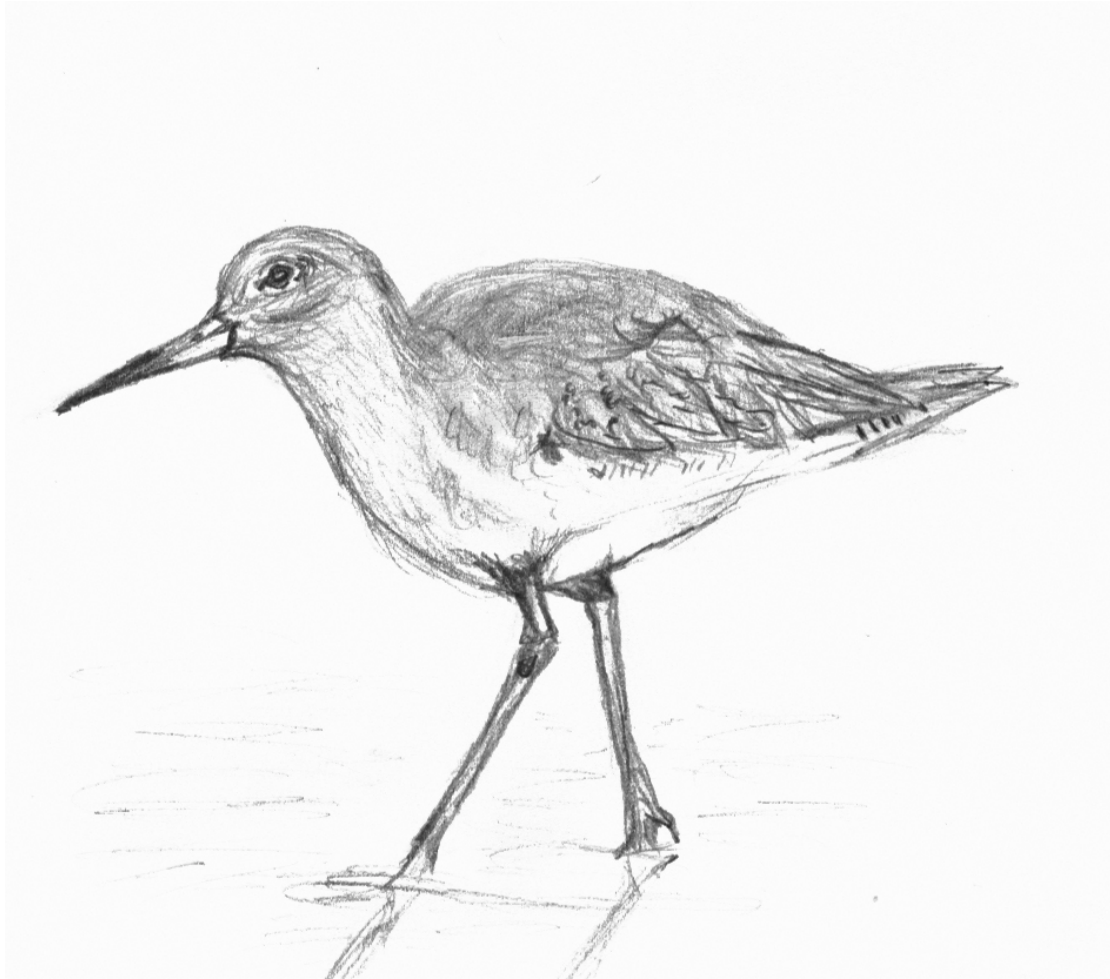
Whitfield, D. P. (2003a). Predation by Eurasian sparrowhawks produces density-dependent mortality of wintering redshanks. *Journal of Animal Ecology* **72**, 27-35.

Whitfield, D. P. (2003b). Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk *Accipiter nisus* predation. *Journal of Avian Biology* **34**, 163-169.

Yasué, M., Quinn, J. L., and Cresswell, W. (2003). Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in redshanks. *Functional Ecology* **17**, 727-736.

CHAPTER 5:

The distribution of overwintering redshanks (*Tringa totanus*) in the Firth of Forth over 12 years with respect to profitability and predation risk: Is there any evidence for a starvation-predation risk trade-off? *



ABSTRACT

Foraging individuals need to meet their energy demands but usually have to do this within a landscape of predation risk. As a consequence, individuals should choose to forage in the least risky environment in which they can meet their energy budget. During colder weather energy demands will increase and some individuals may have to trade-off profitability with predation risk by feeding in more profitable but more risky locations. With climate change and resulting temperature increases, the proportion of individuals having to do this should decline, so reducing the utilisation of riskier habitats. We investigated the way in which temperature affected site choice in overwintering redshanks (*Tringa totanus*) in the Firth of Forth over a 12-year period. We used distance from the shoreline to the low tide and the amount of cover at the shore as indices of actual or perceived predation risk. Sites were classified as being most profitable if they had a muddy substrate. The effects of temperature on distribution were tested at three temporal scales, yearly, monthly and within a few days of counts being made. We predicted that when the weather was colder we would see a shift in the distribution of redshanks away from safe but less profitable sites and into profitable but more risky areas. We found no evidence for any trade-offs between profitability and predation risk related to temperature at the 'year' level. When considering monthly and closely matched temperature effects we found evidence for increased redshank usage of more profitable sites during colder weather and decreased usage of less profitable sites. However, we found no evidence to suggest any trade-off with predation risk: risky profitable sites were not used more at low temperatures. Our findings suggest that redshanks in the Forth estuary currently do not have to trade-off risk with profitability, even during colder weather. More generally it appears that as colder winters become less common, as a result of climate change and if population sizes remain stable, of redshanks and other birds using estuaries are likely to become more widely dispersed across different habitat types.

*I collected 0% of the raw data which comes from the BTO. I carried out 100% of the analysis and 95% of the write-up with my collaborators commenting on and correcting earlier drafts.

INTRODUCTION

Animals must spend a proportion of their time foraging in order to meet their daily energy requirements; but almost always have to do this under risk of predation (Brown and Kotler 2004; Lima 1998b; Lima and Dill 1990; Lind and Cresswell 2005). Consequently, an individual may accept lower foraging intake in order to reduce its risk of predation. This trade-off can manifest itself in many ways, for example through foraging in a group where risk is reduced but where there is competition for food (Beauchamp 1998; Blumstein *et al.* 2001; Lima *et al.* 1999) or by trading-off searching for prey with vigilance (Fitzgibbon 1989; Lima 1987; Lima 1994). Foraging individuals can also respond to actual or perceived risk of predation by avoidance at the landscape level (Cresswell 2008; Lima 1998a). Individuals can choose to forage in habitat patches or areas where predation risk is lower (Gilliam and Fraser 1987; Fraser *et al.* 1995; Abramsky *et al.* 1996; Watts 1991; Krams 1996; Sparrevik and Leonardsson 1995; Rochette and Dill 2000; Altendorf *et al.* 2001; Biro *et al.* 2003); doing so even when safer locations are less profitable foraging areas (Hilton *et al.* 1999; Lima 1990; Todd and Cowie 1990; Cresswell 1994; Kohler and McPeck 1989).

Migrant shorebirds provide a good system in which to examine the starvation-predation risk trade-off. Shorebirds must make decisions about where best to stopover in order to refuel and about where to spend the cold winter months. Individuals must make these decisions in relation to the food attributes of potential foraging areas, because they must meet their energy needs, but should also account for predation risk (Lind 2004). In order to minimise risk some individuals may choose to forage on less profitable areas which also have a lower risk of predation (Pomeroy 2006; Pomeroy *et al.* 2008). During cold weather energetic demands will increase and some individuals may not be able to meet their energy budget in low-risk, low-productivity locations. These individuals may have to trade-off meeting their energy requirements against risk by choosing to forage in high risk, but food rich environments (Cresswell 1994; Yasué *et al.* 2003).

Responses to changes in temperature can occur over different temporal scales. Individuals may show changes in distribution in response to long-term changes in temperature (Maclean *et al.* 2008), and may choose to overwinter on profitable risky

sites only during cold winters. Individuals may also move between foraging areas in response to shorter-term changes in temperature and energy budget (Pederson 1995; Evans 1976), and only choose to forage in profitable but risky areas for short periods within a winter. The spatial scales on which site choice and movements between sites occurs over can range from selecting sites from thousands of kilometres of potential range (Pomeroy *et al.* 2008) and moving hundreds kilometres during a winter (Warnock *et al.* 1995); to making decisions about where to feed within sites over the meter scale (Whitfield 2003). Movements are costly in terms of the energy expenditure of flying any distance, time lost feeding and any potential increase in predation risk; therefore they should only be made when energy budgets cannot be met in a current foraging patch.

Climate change means that long periods of cold weather during the winter are no longer as common as they previously were (in the UK) and are likely to become even less common (Watkinson *et al.* 2004). As winters become warmer, the distributions of overwintering shorebirds are likely to alter; evidence for large-scale shifts in species distributions has already been found (Austin *et al.* 2000; Austin and Rehfish 2005; Maclean *et al.* 2008). It is probable that, on a smaller spatial scale, as cold weather becomes less common, individuals will alter their overwintering locations. With fewer cold periods site choice should be determined less by profitability and possibly more by predation risk. Movements between foraging patches, induced by cold weather, are also likely to become less common.

We investigated the effects of temperature, predation risk and profitability on the distribution of redshanks overwintering in the Firth of Forth in Scotland over a 12-year period. Redshanks do not move over long distances between overwintering areas (Burton 2000; Rehfish *et al.* 2003). However on a smaller spatial scale redshanks have previously been found to trade-off predation risk against profitability by feeding on profitable but risky areas only during cold weather (Cresswell 1994; Cresswell and Whitfield 2008; Yasué *et al.* 2003).

We investigated the effects of temperature, predation risk and profitability on choice of location. When temperatures are higher redshank numbers should decrease with increased risk of predation across both profitable and less profitable foraging areas.

When temperatures are lower, redshank numbers should increase in more profitable areas, especially at those sites that pose a greater risk of predation (which are not normally used) (Figure 5.1).

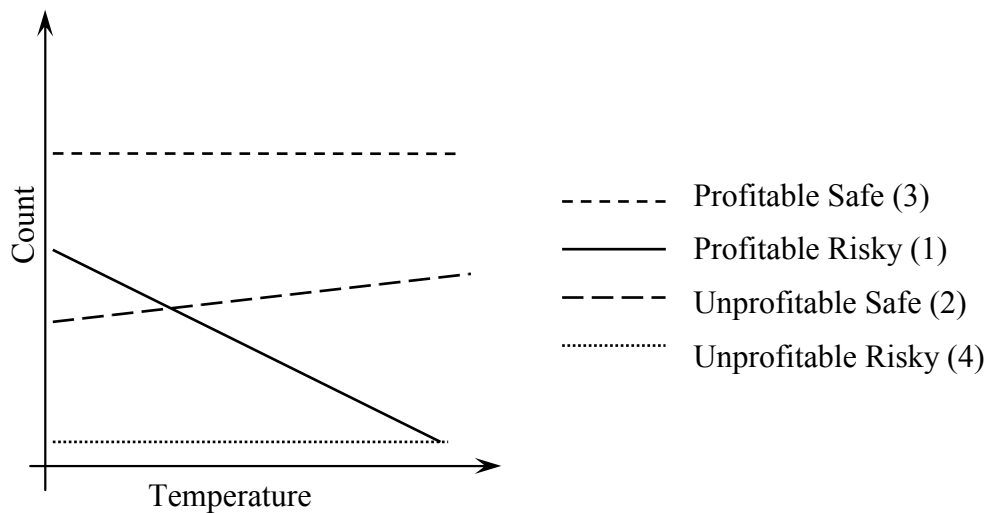


Figure 5.1.

1. Counts in high profitable high risk sites should decrease with temperature because high risk sites are only a good option if starvation risk is high.
2. Low risk, low profitable sites should gain birds as temperature increases because low risk sites are a good option when starvation risk is low.
3. Counts in high profitable, low risk sites should remain similar regardless of temperature as these always provide the best option in terms of foraging and predation risk.
4. Counts in high risk, low profitability sites should also change little with temperature because these always provide the worst option in terms of foraging and predation risk.

METHODS

Study system

The Firth of Forth, on the east coast of Scotland, is a designated special protected area (SPA) with large numbers of overwintering waterbirds. This includes a mean winter population of 3700 redshanks. The estuary comprises of a wide range of intertidal habitats ranging from exposed rock to large sandy bays and mudflats. However at a broad scale the Inner ‘estuarine’ area of the estuary is characterised by large expanses of mud, whereas the outer ‘coastal’ area comprises mainly of rocky shores and sandy bays with some mussel beds. The area covered by this study included the Inner estuary from Kincardine bridge (Skinflats) to the Forth rail and road bridge (between North and South Queensferry) and part of the outer Forth estuary from the bridges east to Ruddons point to the north and Peffer sands to the south (see Figure 5.2).

Site use by redshank in the Firth of Forth

Wetland bird surveys (WeBS) are national counts of wetland birds on major U.K. estuaries. Birds are counted every month during high tide by observers on the shore; for further details of the survey methodology see the British Trust for Ornithology (BTO) web pages (www.bto.org). We obtained WeBS data from the BTO for redshanks in the Firth of Forth over a 12-year period, from the winter of 1994/95 to that of 2005/06. The surveys consisted of one count per month from each year covering the winter period (from November to February). Counts were divided spatially into ‘count sectors’ each of which had a separate total. In addition there were estimates of the total number of redshanks counted in the whole Firth of Forth during each survey. Not every sector was counted in every month of every winter; sectors with large amounts of missing data were excluded from any analysis. The sectors considered for analysis can be seen in Figure 5.2.

Overwintering redshanks are generally site faithful on estuaries (Burton 2000; Rehfish *et al.* 1996; Rehfish *et al.* 2003). Additionally it has been found that redshanks in the Firth of Forth remain in the same area during the winter and that roosting and feeding sites are similar (Symonds and Langslow 1984). Therefore the distribution of redshanks at high tide should reflect that at low tide, assuming redshanks do not travel large distances between foraging and roosting sites. In order to test this we compared the high tide distribution of redshanks with that at low tide

during the winter of 2003/04. Low tide survey data from the Firth of Forth were obtained from the BTO for the winter of 2003/04. Redshanks were counted monthly from November to February. Count sectors were smaller, but data from these was aggregated to produce low tide counts, which corresponded spatially to the WeBS count sectors. These counts were used to compare the high and low tide distribution of redshanks at 17 sites with sufficient data to determine if low tide foraging locations of redshanks closely matched the distribution at high tide.

Index of predation risk

Sparrowhawks (*Accipiter nisus*), and other raptors, which prey on redshanks, are more likely to be successful when they attack from concealing cover (Cresswell 1996; Whitfield 1985; Whitfield 2003); more open areas far from cover may also increase redshanks ability to detect predators such as peregrine falcons (*Falco peregrinus*). Therefore the further from cover that a redshank can forage the lower its risk of predation. Raptor concealing cover occurs at the shoreline of coastal and estuarine sites. This means sites with more habitat available far from cover (i.e. sites with a large distance from the shore to the water) should have, or be perceived by redshanks to have, a lower risk of predation (Cresswell 2008; Lima 1998a; Pomeroy *et al.* 2008). A secondary index of predation risk may also be the amount of tree-cover at the shoreline because this is likely to provide the most effective form of concealment for raptors (Cresswell 1996). Therefore sites with tree-cover on a larger proportion of the shoreline should provide more opportunities for raptors to launch more effective surprise attacks on redshanks.

Index of profitability

The intertidal habitats of count sectors were broadly classified as being a mudflat, or an area of sandy beach and of rocky shore (characterised by bare rock, seaweed covered rock and sandy inlets). Mud is likely to be a food rich environment providing a profitable foraging substrate for redshanks; in comparison, sandy and rocky areas are likely to be less profitable to foraging redshanks. This is reflected in redshanks preference to overwinter in muddy areas (Hill *et al.* 1993); and in the dietary preferences of redshanks, which tends towards prey species found in muddy substrates such as *Corophium sp.* (Goss-Custard 1969).

Measuring sector Characteristics

Ordnance survey maps of the Firth of Forth, at the scale of 1:25000, were used in order to establish the profitability and perceived and/or actual predation risk at each count sector. Percentage tree-cover at the shoreline, and main substrate of sectors (muddy or non-muddy) were estimated directly from the maps. The mean distance from the shoreline to the mean low tide line was calculated from the mean of four measurements of this distance. The measurements of distance to mean low tide were taken at equally spaced intervals along the shoreline of each sector. These measurements were made in MapInfo (version 6.0) using a digitised ordnance survey map. The area of each sector was measured in MapInfo by drawing a polygon for each sector using the ordnance survey map as a template.

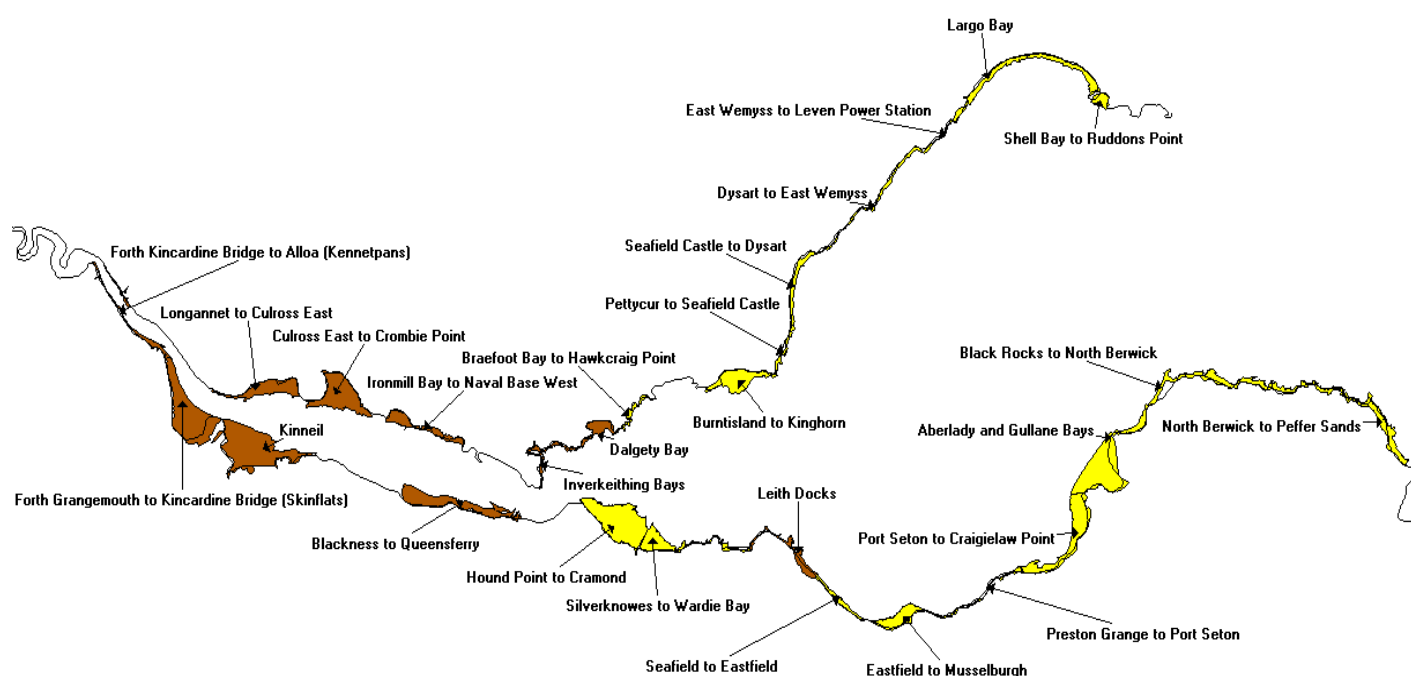


Figure 5.2. Map showing names, locations, size and major substrate of WeBS count sectors on the forth. Sites showed in brown are muddy whilst those in yellow consist of sandy and rocky areas. As can be seen the Inner Forth is mainly comprised of muddy areas whilst the shore of outer Forth contains rocky and sandy substrates.

Weather data

Weather data from a Met Office weather station located at Braefoot Bay on the Firth of Forth (Figure 5.2) was obtained from the British Atmospheric Data Centre (BADC). The data consisted of daily mean minimum temperatures for the whole 12-year period. From this the number of ‘frost days’ (days where the minimum temperature was at 0°C or below) in each year and in each month could be calculated.

In order to investigate the effects of temperature on distribution on a more closely matched time scale, the mean minimum temperature was calculated over three days, from two days before to and including the day of the survey.

Model Parameters

We simplified the names of some of our model variables for clarity, as follows:

Cover Risk= Percentage cover at the shore per sector.

Distance Risk=Mean distance from the shoreline to the mean low tide line at each sector.

Profitability=Determined by the substrate of a sector, where 1=Muddy and most profitable and 0=Sandy/rocky and less profitable.

Total monthly count=Total count from all sectors in the Firth of Forth (i.e. an index of population size at the time of each survey).

Other variables modelled were the year and month in which the counts were conducted; the sector the count was made in and the area of each sector. Temperature was considered at three temporal levels, yearly, monthly and within 3 days of each count (including the day of the count). At the yearly and monthly level the number of frost days was used as an index of cold weather. At the more closely matched level mean minimum temperature was used.

Analysis

High and low tide distributions were compared for the winter of 2003/04. Winter means at 17 WeBS sectors, with sufficient data, were calculated from WeBS (high tide) and low tide surveys. A linear regression was then carried out in SPSS (version 12) to investigate if high tide distribution was a good predictor of low tide distribution (at the spatial level of sectors).

The effects of temperature, risk and profitability on distribution were modelled using generalised estimating equations (GEEs). Analysis was conducted using SAS (version

9.2). To account for the fact that repeated counts were made in the same sectors every month and over 12 years ‘Count sector’ was included as the repeated variable using an exchangeable correlation structure (i.e. all counts within sectors are equally likely to be correlated with one another). Log of site area was used as an offset to account for ‘effort’ effects (i.e. more birds are likely to be counted in larger areas). The count data being modelled were overdispersed; therefore a Poisson scaling factor was also included in all models.

We wanted to investigate which models provided the best fit for our data, but also which would provide us with the most ‘biologically meaningful’ test of our hypotheses. To do this we investigated the significance of all model parameters using the chi-squared analysis for the ‘full’ GEE models (i.e. with all parameters in the model). We then removed non-significant variables one parameter at a time. For the full model and every subsequent model we calculated the QICu value. This is a measurement for goodness of fit similar to Akaike’s information criterion but for quasi-likelihood modelling methods, where a lower QICu value indicates a better fit to the data (Hardin and Hible 2003; Pan 2001). For each step the significance of each parameter was reassessed. Model selection continued until all variables that were non-significant or not close to significance were removed; or until further model reduction greatly increased the QICu value of the model. Models were sorted in ascending order of QICu and the change in QICu comparing the ‘top’ model (i.e. the model with the lowest QICu) to all others was calculated. Models that differed from the ‘top’ model in QICu by less than 4, were considered to be substantially equivalent in terms of goodness of fit (Burnham and Anderson 2002). The significance values of the model parameters were compared in any models that provided an equivalent goodness of fit to the data. This was done to assess which models provided the best test of our hypotheses in terms of biological significance. Once a model had been selected, its biological implications were further investigated by consideration of its parameter estimates.

RESULTS

Comparison of high and low tide distributions

Counts of redshanks at high and low tide in the winter of 2003/04 were compared across 17 sites with enough available data. High and low tide distributions were found to be very similar (Figure 5.3). A linear regression found high tide counts were a good predictor of counts at low tide ($R^2=0.84$), (Figure 5.4).

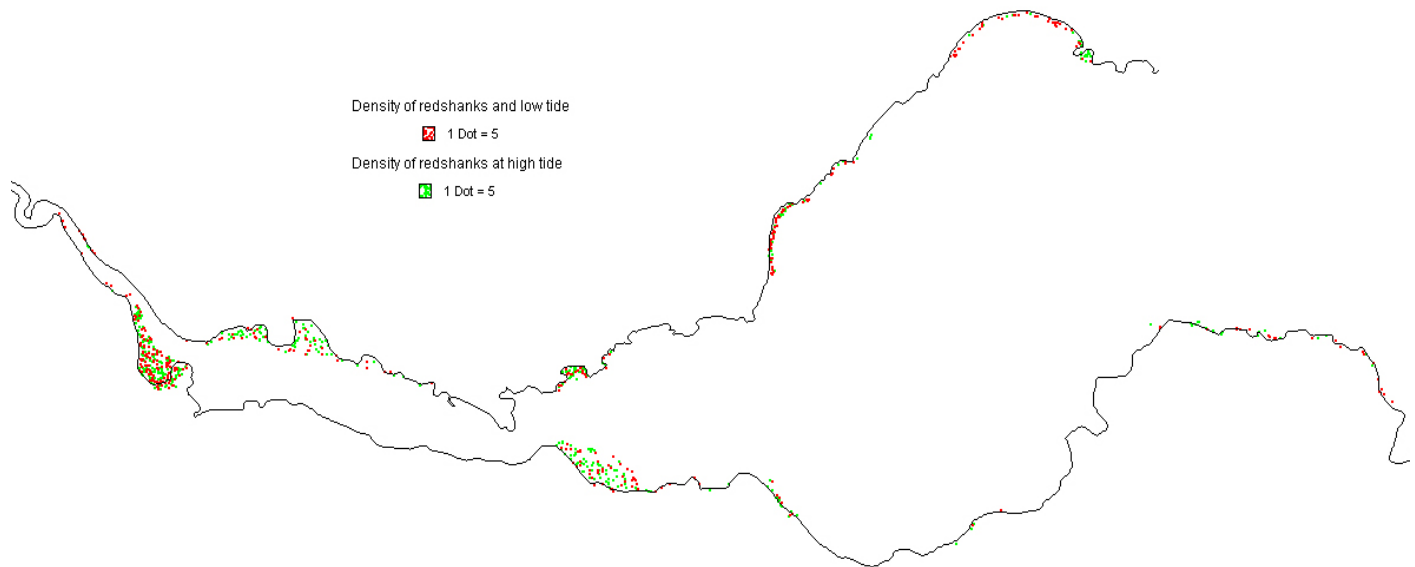


Figure 5.3. Comparison of the numbers of redshank counted at 17 sites on the Firth of Forth at high and low tide in the winter of 2003/04. Each dot represents 5 redshanks, dots are concentrated in the 17 count sectors where distributions were compared, but are placed randomly within these.

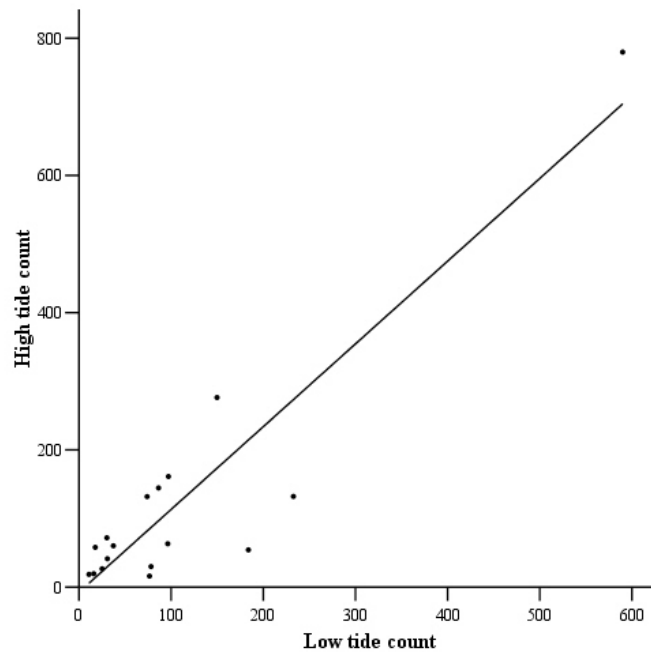


Figure 5.4. Scatter graph showing the relationship between counts at high and low tide at 17 sites in the Firth of Forth in the winter of 2003/04. Line is linear regression fitted to the data ($y=1.21x - 7.30$, $F_{1,16}=80.28$, $p<0.001$), with the outlier removed ($y=0.58x + 36.38$, $F_{1,15}=5.48$, $p=0.035$).

Yearly temperature effects on redshank distribution

There was some variation between years, in terms of the number of frost days, with the lowest number in a year being 16 days and the highest 39 days; but many years were broadly similar having between 28 and 35 frost days (see Appendix 1 Table 1).

There were no significant interactions between the number of frost days in each year and the measures of site riskiness and substrate type (as an indicator of profitability) (Table 5.1). Removal of the non-significant three-way interaction did not result in any significant two-way interactions. There was no evidence for a temperature dependant effect in the number of redshanks using sites in relation to risk attributes and profitability, when considering variation in cold weather between years; therefore no model selection was conducted and no further analysis of yearly temperature effects was carried out.

Table 5.1. Type III analysis for a generalised estimating equation investigating the effect of yearly variation in cold weather on the monthly counts of redshanks in count sectors on the Firth of Forth in relation to predation risk at and profitability of sites. Significant P values are marked in bold.

Model Factor	DF	Chi-Square	P value
Month	3	8.48	0.037
frost days in a year	6	9.02	0.172
Total monthly count	1	0.17	0.683
Distance Risk	1	0.05	0.816
Cover Risk	1	0.62	0.431
Profitability	1	0.80	0.373
frost days in a year*Profitability	6	11.02	0.088
frost days in a year*Distance Risk	6	7.99	0.239
frost days in a year*Cover Risk	6	5.21	0.518
Distance Risk*Profitability	1	2.67	0.103
Distance Risk*frost days in a year*Profitability	14	15.40	0.351

Investigation of monthly measures of temperature on redshank distribution

Within each year there was some variation in temperature between months. In some months no frost days were recorded compared to other months in the same year with a number of days when the temperature was below zero (e.g. up to 14 days). Matched minimum temperatures also varied between months in the same year, for example varying from -0.54°C up to 5.3°C in one winter (see Appendix 1, Table 2).

Frost days in a month

A generalised estimating equation investigating the effects of variation in frost days at a monthly level showed some evidence for changes in redshank counts that were dependant on predation risk and profitability of sites. Several interactions between risk and temperature were found to be significant or close to significance, therefore model selection was carried out (Table 5.2). We found no evidence for including a three-way interaction between temperature, risk and profitability because models containing this interaction had much higher QICu values than models where this

interaction is removed. Therefore we have no evidence for redshanks altering their site use during cold weather in relation to tradeoffs between risk and profitability (i.e. for different slopes of the lines illustrated in Figure 5.1).

Table 5.2. Testing the goodness of fit of models investigating the effect of monthly variation in temperature on monthly counts in sectors, in relation to profitability and risk, as non-significant model parameters were removed. Models are ordered by descending QICu, with the model providing the ‘best’ fit to the data appearing first.

Model	QICu	Change in QICu
Month + Frost days + Profitability + Distance Risk + Cover Risk+ Frost days*Profitability + Frost days* Distance Risk + Frost days* Cover Risk+ Distance Risk *Profitability	-14486.04	0
Month + Total count + Frost days + Profitability + Distance Risk + Cover Risk+ Frost days*Profitability + Frost days* Distance Risk + Frost days*Cover Risk+ Distance Risk *Profitability	-14482.37	3.67
Winter year + Month + Total count + Frost days + Profitability + Distance Risk + Cover Risk+ Frost days*Profitability + Frost days* Distance Risk + Frost days* Cover Risk+ Distance Risk *Profitability	-14476.12	9.92
Winter year + Month + Total count + Frost days + Profitability + Distance Risk + Cover Risk+ Frost days*Profitability + Frost days* Distance Risk + Frost days* Cover Risk+ Distance Risk *Profitability + Distance Risk *Profitability*Frost days	-14462.03	24.01
Month + Frost days + Profitability + Distance Risk + Cover Risk+ Frost days*Profitability + Frost days* Distance Risk + Frost days* Cover Risk	-13713.55	772.49

The models with the lowest QICu value all contained interactions between frost days and profitability of sites, and at least one of our measures of risk. The two top models had similar QICu values (Burnham and Anderson 2002) and therefore both were investigated further using the chi-squared analysis of the generalised estimating equations. In Table 5.3 it can be seen that these models are very similar, and that removal of total count has little effect, therefore we consider the simplest model with the fewest parameters for further investigation.

Table 5.3. Type III data analysis for the top two models ranked using QICu.

Significant P values are marked in bold.

Model Factor	D.F.	Chi-Square		P value	
		Model 1	Model 2	Model 1	Model 2
Month	3	8.88	8.95	0.031	0.03
Total count	1	-	1.53	-	0.216
Frost days	1	1.81	1.85	0.178	0.174
Profitability	1	0.80	0.80	0.371	0.372
Distance Risk	1	1.88	1.87	0.17	0.171
Cover Risk	1	0.68	0.71	0.41	0.40
Frost days*Profitability	1	5.94	5.83	0.015	0.016
Frost days* Distance Risk	1	3.6	3.59	0.058	0.058
Frost days* Cover Risk	1	2.9	2.88	0.089	0.09
Distance Risk *Profitability	1	1.15	1.14	0.284	0.285

There was no significant effect of risk (either in terms of percentage cover at the shore or distance from cover) on redshank counts (Tables 5.3 and 5.4). We found no significant interaction between risk and profitability (Table 5.3), which suggests that the response to risk is similar in profitable and less profitable foraging areas.

Redshank counts varied significantly with month reflecting the fact that fewer redshanks were counted in January and February compared to November and December. The relationship between redshank count and substrate (profitability) was dependent on the number of frost days (energetic demands) (Table 5.4). The parameter estimate for the interaction between frost days and substrate suggested that redshank numbers on less profitable (non-muddy) sites decrease relative to those on profitable (muddy) sites, as it gets colder. Although the relationship between redshank count and predation risk (either mean distance from the shore or percentage cover at shore) were marginally dependent on the number of frost days (energetic demands), the biological effect is extremely small (i.e. parameter estimates very close to zero). Note that the overall relationships between profitability and temperature with redshank numbers cannot be meaningfully interpreted from the main effects in this model given the significant interaction between profitability and the number of frost days.

Table 5.4. Parameter estimates for the generalised estimating equation of model 2.
Significant terms are marked in bold.

Model parameter	Factor level	Estimate	Standard error
Intercept		3.752	0.279
Month	1	-0.162	0.059
Month	2	-0.195	0.046
Month	11	0.020	0.077
Month	12	0	0
frost days		-0.004	0.009
Profitability	0	0.386	0.418
Profitability	1	0	0
Distance Risk		0.001	0.000
Cover Risk		-0.004	0.005
frost days*Profitability	0	-0.020	0.006
frost days*Profitability	1	0	0
frost days* Distance Risk		0.000	0.000
frost days* Cover Risk		-0.000	0.000
Distance Risk*Profitability	0	-0.001	0.001
Distance Risk*Profitability	1	0	0

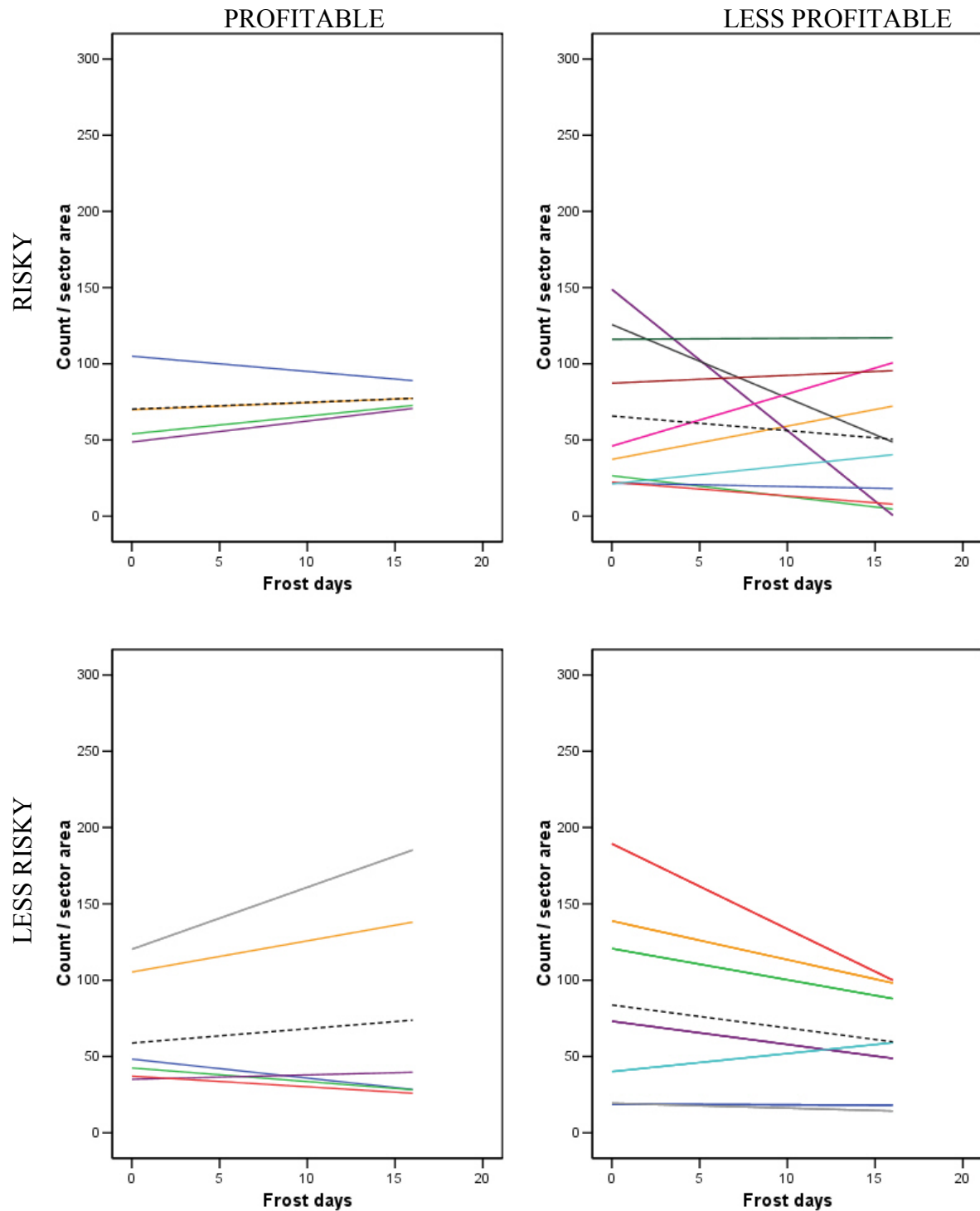


Figure 5.5. An illustration of the way in which redshank counts change with temperature dependant on predation risk and profitability at sites in the Firth of Forth. Plots show trend-lines for the change in density (count per km²) of redshanks with increased number of frost days (i.e. decreasing temperature). Sites were split into the four categories represented in each panel based on profitability and predation risk (i.e. the 4 predictions illustrated in Figure 5.1). Sites were classified as risky if the distance from shore to low tide line was less than or equal to the median of 300 meters. Those with a greater distance from the shore to low tide were considered less risky. The coloured lines denote trends for each site (each site appears exclusively in one category), and the dashed line represents the overall trend in each category. Lines are linear regression fitted to the data; data points have been removed to clearly show the trends in the relationship between count and temperature.

We investigated the way in which redshank numbers varied with temperature dependent on site profitability and predation risk by examining trends in count numbers at each site with temperature (Figure 5.5). Although there was some variation in trends between sites it appears that, overall, the number of redshanks counted at less profitable sites decreased with colder weather. There is also evidence to suggest that redshank numbers probably increased at profitable sites in colder weather, although this is less clear. This suggests redshanks foraged on less profitable sites during milder weather and more profitable sites during cold weather. There was no overall effect of risk on redshank numbers in relation to variation in temperature as the trends for change in redshank numbers with frost days are in opposing directions within each category of risk, confirming the findings of our models.

Matched minimum temperature

Evidence for significant or near to significant interactions between redshanks distribution and risk, profitability and matched minimum temperature was found, therefore model selection was carried out (Table 5.5). When considering goodness of fit of models with non-significant parameters removed (Table 5.5), the change in QICu value suggested that the 'top model' provided a better fit for the data when compared to other models, therefore we investigated this model further.

Table 5.5. Testing the goodness of fit of models investigating the effect of short-term variation in temperature on monthly counts in sectors, in relation to profitability and risk, as non-significant model parameters were removed. Models are ordered by descending QICu, with the model providing the ‘best’ fit to the data appearing first.

Model	QICu	Change in QICu
Month + Distance Risk + Matched minimum temperature + Profitability + Cover Risk+ Matched minimum temperature *Profitability + Matched minimum temperature * Distance Risk + Distance Risk *Profitability	-13794.54	0
Month +Total count + Distance Risk + Matched minimum temperature + Profitability + Cover Risk+ Matched minimum temperature *Profitability + Matched minimum temperature * Distance Risk + Distance Risk *Profitability	-13785.47	9.07
Winter year + Month +Total count + Distance Risk + Matched minimum temperature + Profitability + Cover Risk+ Matched minimum temperature *Profitability + Matched minimum temperature * Distance Risk + Distance Risk *Profitability	-13740.82	53.72
Winter year + Month + Total count + Distance Risk + Matched minimum temperature + Profitability + Cover Risk+ Matched minimum temperature *Profitability + Matched minimum temperature * Distance Risk + Matched minimum temperature * Cover Risk+ Distance Risk *Profitability + Distance Risk *Profitability* Matched minimum temperature	-13732.21	62.33
Winter year + Month + Total count + Distance Risk + Matched minimum temperature + Profitability + Cover Risk+ Matched minimum temperature *Profitability + Matched minimum temperature * Distance Risk + Matched minimum temperature * Cover Risk+ Distance Risk *Profitability	-13716.45	78.09
Month + Distance Risk + Matched minimum temperature + Profitability + Cover Risk+ Matched minimum temperature *Profitability + Matched minimum temperature * Distance Risk	-12950.75	843.79

There was no evidence for a change in redshank numbers with temperature that was dependant on a trade-off between predation risk and profitability (i.e. a three way interaction, Tables 5.5 and 5.6). There was also no significant interaction between risk and profitability suggesting that redshanks respond to risk in the same way at profitable and less profitable sites (Table 5.5). Again there was no significant effect of risk on site usage (Table 5.6). In model 1 (Table 5.6) there was a significant interaction between matched minimum temperature and profitability, which suggests that the change in the number of redshanks counted with temperature is dependant on profitability of a site. There was also a significant variation in counts with month.

Table 5.6. Type III data analysis for the top model based on QICu. Significant P values are marked in bold.

Model Factor	D.F.	Chi-Squared	P
month	3	9.55	0.023
Profitability	1	0.27	0.601
Distance Risk	1	2.71	0.1
Cover Risk	1	0.88	0.347
matched minimum temperature	1	1.38	0.24
matched minimum temperature*Profitability	1	4.75	0.029
matched minimum temperature* Distance Risk	1	2.09	0.149
Distance Risk *Profitability	1	1.67	0.196

The parameter estimates for the best fitting model are shown in Table 5.7. These are very similar to those for the model investigating the effects of frost days. . The effect of month in the model is also the same with fewer redshanks in January and February. The parameter estimate for the interaction between minimum temperature and profitability suggests that redshank numbers on less profitable sites increased with increased temperature relative to those on profitable sites.

Table 5.7. Parameter estimates for the generalised estimating equation of model 2. Significant terms are marked in bold.

Model parameter	Factor level	Estimate	Standard error
Intercept		3.689	0.297
month	1	-0.162	0.056
month	2	-0.206	0.051
month	11	0.047	0.080
month	12	0	0
Profitability	0	0.228	0.434
Profitability	1	0	0
Distance Risk		0.001	0.0002
Cover Risk		-0.005	0.005
matched minimum temperature		-0.008	0.013
matched minimum temperature *Profitability	0	0.042	0.008
matched minimum temperature *Profitability	1	0	0
matched minimum temperature * Distance Risk		0.000	0.000
Distance Risk*Profitability	0	-0.001	0.001
Distance Risk*Profitability	1	0	0

The change in redshank numbers with minimum temperature on profitable and less profitable site was further considered in the same way as with frost days. Figure 5.6 shows the trends in redshanks numbers with increasing minimum temperature, depending of profitability and also on predation risk (in terms of meters from the shore to the mean low tide line). Despite some variation between sites, it appears that overall the number of redshanks counted at less profitable sites probably decreased with colder weather. The data also suggest that redshank numbers increased slightly at profitable sites in colder weather, although this is a less clear. Again, there was no evidence to suggest predation risk influences the way in which redshank numbers vary with temperature.

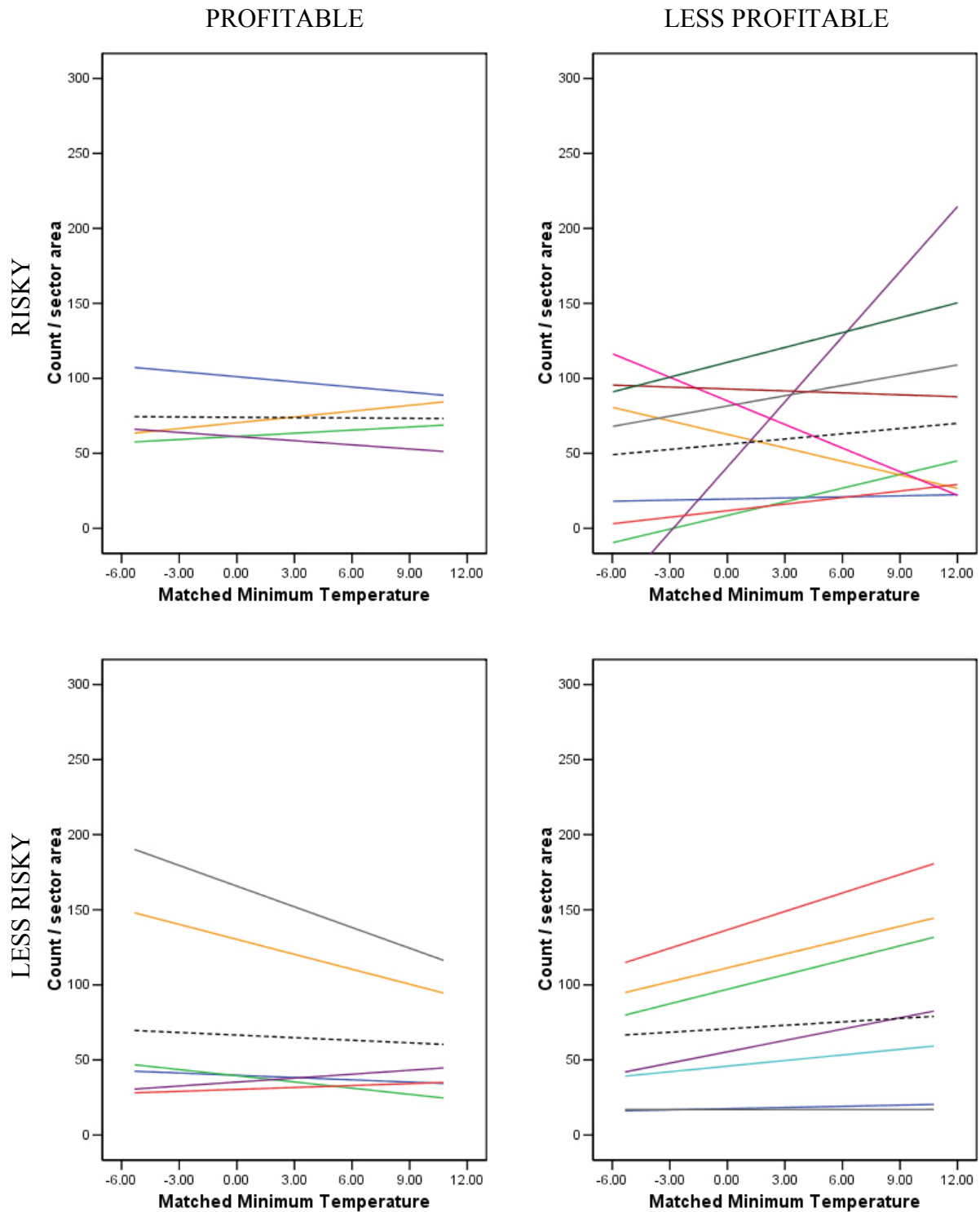


Figure 5.6. An illustration of the way in which redshank counts change with temperature dependant on predation risk and profitability at sites in the Firth of Forth. Plots show trend-lines for the change in the density (count per km²) of redshanks with change in matched minimum temperature. Sites were split into the four categories represented in each panel based on profitability and predation risk (i.e. the 4 predictions illustrated in Figure 5.1). Sites were classified as risky if the distance from shore to low tide line was less than or equal to the median of 300 meters. Those with a greater distance from the shore to low tide were considered less risky. The coloured lines denote trends for each site (each site appears exclusively in one category), and the dashed line represents the overall trend in each category. Lines are linear regression fitted to the data; data points have been removed to show clearly the trends in the relationship between count and temperature.

DISCUSSION

We found no evidence for any temperature related, between-year changes in redshank distribution. Redshanks, however, altered their habitat use with monthly variation in cold weather and also with changes in temperature within a few days of when counts were conducted. This confirms that redshanks can change their distribution, to some degree, in a flexible way in response to medium and short-term changes in temperature and energy demands (Yasué *et al.* 2003). This also provides confirmation that, to some extent, redshanks do move between sites. This is important when interpreting the first result, that the distribution of redshanks has not varied with temperature over the 12-year period covered in this study. If, redshanks never respond to variation in temperature by altering their foraging location, or the population is at carrying capacity across all habitat types, which would preclude any movement, then we could not effectively test for, or detect any effect of climatic changes on redshank distribution. However, having demonstrated a response to temperature within winters, the lack of a change between winters is likely to be because climate change has had little effect over the period of the study. Redshanks should always remain in the least risky patches as long as they can meet their energy budgets there (Yasué *et al.* 2003; Sansom *et al.* 2009). Once winters are warm enough for all redshanks to be able to occupy low risk sites, further systematic long-term temperature changes should not change their distribution. Given the effects of climate change on recent winter temperatures (Watkinson *et al.* 2004) all winters covered in this study may have already been too 'warm' to result in further changes in distribution. For example the average number of frost days between 1961-1990 in Edinburgh was 42.2 (Met office data) compared to a mean of 30.7 over the 12 years of this study.

In contrast, the occurrence of cold weather periods within winters was found to affect where redshanks chose to feed in relation to profitability, although to a relatively small degree. Greater numbers of redshanks were found to use less profitable sites as temperatures increased and there was a tendency towards increased numbers at more profitable sites in cold weather. This was probably due to the change in the amount of energy individuals needed in different weather conditions. During warmer weather, when starvation risk is lower, sites that are low in risk but are less profitable provide a good choice of foraging location in terms of minimising predation risk without compromising energy intake. Because individual redshanks are likely to vary in

foraging efficiency (Caldow *et al.* 1999), during colder weather some individuals from less profitable areas, may have been forced to move to forage in the more profitable areas (Cresswell 1994; Pomeroy *et al.* 2008; Yasué *et al.* 2003). Given that large numbers of redshanks are always likely to forage on highly profitable low risk areas, these additional individuals only had a small effect on overall counts in such areas.

The observed shift in redshank distribution between foraging areas differing in profitability, in response to starvation risk is consistent with that fact that individual animals often respond to changes in energy budget and starvation risk by moving to more productive foraging patches (Evans 1976; Hilton *et al.* 1999; Warnock *et al.* 1995). Such movements could be into areas that provide richer food sources (Dugan 1982; Cresswell 1994), or environments in which an individual can forage more effectively, for example away from competition (Goss-Custard 1980; McNamara 1982).

Although redshanks moved between different areas, depending on profitability, in response to relatively short-term variation in temperature, they did this without increasing their risk of predation (in terms of distance from predator concealing cover).. So why do we not observe any need for individuals to use risky but profitable sites? There are five likely main reasons.

Firstly, predation risk may have been traded-off with starvation risk in other ways that we have not considered. Individuals may have responded to increased starvation risk by altering their foraging behaviour within a habitat patch rather moving to different areas, which varied in risk, for example, through variation in time spent foraging altering time that can be spent on vigilance (Whittingham and Evans 2004; Arenz and Leger 2000; McNamara and Houston 1994). Secondly, there may be a high availability of low risk but profitable habitat, which provides a high quality foraging option to large numbers of redshanks even during cold weather. Thirdly, the periods of cold weather experienced by redshanks may not have increased energy budgets to a level where large numbers of individuals were competing for profitable foraging but safe foraging locations, and hence few individuals were forced to trade-off safety for

food in riskier areas. Additionally redshanks maybe constrained from moving between areas due to competition with other species, high densities of other birds are likely to forage on profitable muddy sites and these may exclude redshanks. Finally, there may have been only very few sites that were both profitable and posed a high risk of predation, or that these were used by only very small numbers of birds during cold weather, so that we were unable to detect the very small effect this would have on the overall distribution. All or some of these potential explanations could apply of course. Regardless of which did apply, our results demonstrate however that redshanks in the Firth of Forth are currently not forced to use risky sites even in cold weather.

Our results here contrast with the finding, on a smaller spatial scale along the Fife coast, that redshanks did not move between sites during cold weather. This may reflect a more variable and perhaps greater starvation risk experienced by redshanks in the Firth of Forth over the period of this study (Yasué *et al.* 2003). Additionally the scale and habitat composition of the areas covered also differed between the two studies; in Fife we investigated movements within coastal areas, whereas in the Firth of Forth we investigated movements on a larger scale, across estuarine and coastal areas. This may mean that differences in the availability of highly profitable low risk habitat or in population density affected whether or not movements occurred (Dowding and Chamberlin 1991; McNamara 1982). If the population density was higher or highly profitable habitat was limited on the Fife coast, movements may be limited because the best sites were fully occupied, whereas those in the Firth of Forth are not, thus allowing for movements during cold weather (Goss-Custard 1985; Goss-Custard *et al.* 1996). Another explanation may be differences in the populations of redshanks wintering in the two areas. The age profile of the two populations may differ or Fife coastal birds may largely be from British breeding populations, whereas those in the Firth of Forth are a mixture of British and Icelandic birds. There may be sub-specific or age-related differences in habitat use, site fidelity and propensity to respond to weather through movement rather than behavioural trade-offs (Cresswell 1994; Broton *et al.* 2000) .

As winters have become milder, as a result of climate change, our findings suggest that within estuaries there may be fewer temperature related movements, and overwintering populations of redshanks have become more evenly spread across

different habitat types. As starvation risk is reduced so more habitats become suitable for a species, because even very unprofitable but safe habitats can be used. This is a reflection of the larger scale UK wide response in overwintering shorebirds, whereby warmer winters have allowed populations to exploit eastern coasts that would previously have posed a greater starvation risk (Austin and Rehfisch 2005). Without strong energy budget constraints redshanks should choose overwintering locations based entirely on predation risk throughout the winter. However, it is important to remember that predators are then also likely to respond to such changes in the behaviour of their prey. If redshanks become less concentrated on particular food-rich sites within estuaries it is likely that predator hunting behaviour will be affected (Cresswell 2008; Lima 1998a). Predators may spread their hunting efforts more evenly across habitats matching the redshanks distribution, may use different hunting strategies or change the composition of the species on which they prey. Prey may then have to respond in turn. When investigating the impact climate change will have on overwintering populations of shorebirds it is therefore important that changes in and responses to predation risk are also considered.

REFERENCES

- Abramsky, Z., Strauss, E., Kotler, B. P., Riggs, G., and Riechman, A. (1996). The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G.pyramidum*. *Oecologia* **105**, 313-319.
- Altendorf, K. B., Laundre, J. W., Gonzalez, C. A. L., and Brown, J. S. (2001). Assessing effects of predation risk on the foraging behaviour of mule deer. *J.Mammal.* **82**, 430-439.
- Arenz, C. L. and Leger, D. W. (2000). Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. *Animal Behaviour* **59**, 535-541.
- Austin, G. E., Peachel, I., and Rehfisch, M. M. (2000). Regional trends in coastal wintering waders in Britain. *Bird Study* **47**, 352-371.
- Austin, G. E. and Rehfisch, M. M. (2005). Shifting nonbreeding distributions of migratory fauna in relation to climatic change. *Global Change Biology* **11**, 31-38.

- Beauchamp, G. (1998). The effect of group size on mean food intake rate in birds. *Biological Reviews of the Cambridge Philosophical Society* **73**, 449-472.
- Biro, P. A., Post, J. R., and Parkinson, E. A. (2003). Population consequences of a predator-induced habitat shift by trout in whole-lake experiments. *Ecology* **83**, 691-700.
- Blumstein, D. T., Daniel, J. C., and Evans, C. S. (2001). Yellow-footed rock-wallaby group size effects reflect a tradeoff. *Ethology* **107**, 655-664.
- Broton, L., Orell, M., Lahti, K., and Koivula, K. (2000). Age-related microhabitat segregation in willow tit *Parus montanus* winter flocks. *Ethology* **106**, 993-1005.
- Brown, J. S. and Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters* **7**, 999-1014.
- Burnham, K. P. and Anderson, D. R. (2002). 'Model selection and multimodel inference: A practical information-theoretic approach.' (Springer: New York.)
- Burton, N. H. K. (2000). Winter site-fidelity and survival of Redshank *Tringa totanus* at Cardiff, south Wales. *Bird Study* **47**, 102-112.
- Caldow, R. W. G., Goss-Custard, J. D., Stillman, R. A., Le V. D. Durell, S. E. A., Swinfen, R., and Bregnballe, T. (1999). Individual variation in the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and susceptibility to interference. *Journal of Animal Ecology* **68**, 869-878.
- Cresswell, W. (1994). Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *Journal of Animal Ecology* **63**, 589-600.
- Cresswell, W. (1996). Surprise as a winter hunting strategy in Sparrowhawks *Accipiter nisus*, Peregrines *Falco peregrinus* and Merlins *F. columbarius*. *Ibis* **138**, 684-692.
- Cresswell, W. (2008). Non-lethal effects of predation in birds. *Ibis* **150**, 3-17.

- Cresswell, W. and Whitfield, D. P. (2008). How starvation risk in Redshanks *Tringa totanus* results in predation mortality from Sparrowhawks *Accipiter nisus*. *Ibis* **150**, 209-218.
- Dowding, J. E. and Chamberlin, S. P. (1991). Annual movement patterns and breeding-site fidelity of the New Zealand Dotterel (*Charadrius obscurus*). *Notornis* **38**, 89-102.
- Dugan, P. J. (1982). Seasonal changes in patch use by a territorial grey plover: weather-dependent adjustments in foraging behaviour. *Journal of Animal Ecology* **51**, 849-857.
- Evans, P. R. (1976). Energy balance and optimal feeding strategies in waders: some implications for their distribution and movements in the non-breeding season. *Ardea* **64**, 117-139.
- Fitzgibbon, C. D. (1989). A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Animal Behaviour* **37**, 508-510.
- Fraser, D. F., Gilliam, J. F., and Yip-Hoi, T. (1995). Predation and an agent of population fragmentation in a tropical watershed. *Ecology* **76**, 1461-1472.
- Gilliam, J. F. and Fraser, D. F. (1987). Habitat selection when foraging under predation hazard: a model and a test with stream-dwelling minnows. *Ecology* **68**, 1856-1862.
- Goss-Custard, J. D. (1969). The winter feeding ecology of the redshank *Tringa totanus*. *Ibis* **111**, 338-356.
- Goss-Custard, J. D. (1980). Competition for food and interference among waders. *Ardea* **68**, 31-52.
- Goss-Custard, J. D. (1985). Foraging behaviour of wading birds and the carrying capacity of estuaries. In 'Behavioural Ecology: Ecological Consequences of Adaptive Behaviour.' (Eds R. M. Sibly and R. H. Smith.) pp. 169-188. (Blackwell Scientific Publications: Oxford.)

- Goss-Custard, J. D., West, A. D., Clarke, R. T., and Le V. Dit Durell, S. E. A. (1996). The carrying capacity of coastal habitats for oystercatchers. In 'The Oystercatcher: from individuals to populations.' (Ed J. D. Goss-Custard.) pp. 327-351. (Oxford University Press: Oxford.)
- Hardin, J. W. and Hible, I. (2003). 'Generalized Estimating Equations.' (Chapman and Hall).
- Hill, D., Rushton, S. P., Clark, N., Green, P., and Prys-Jones, R. (1993). Shorebird communities on British estuaries: factors affecting community composition. *Journal of Applied Ecology* **30**, 220-234.
- Hilton, G. M., Ruxton, G. D., and Cresswell, W. (1999). Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. *Oikos* **87**, 295-302.
- Kohler, S. L. and McPeck, M. A. (1989). Predation risk and the foraging behaviour of competing steam insects. *Ecology* **70**, 1181-1825.
- Krams, I. A. (1996). Predation risk and shifts of foraging sites in mixed willow and crested tit flocks. *Journal of Avian Biology* **27**, 153-156.
- Lima, S. L. (1987). Vigilance while feeding and its relation to the risk of predation. *Journal of Theoretical Biology* **124**, 303-316.
- Lima, S. L. (1990). Protective cover and the use of space: different strategies in finches. *Oikos* **58**, 151-158.
- Lima, S. L. (1994). On the personal benefits of anti-predatory vigilance. *Animal Behaviour* **48**, 734-736.
- Lima, S. L. (1998a). Nonlethal effects in the ecological effects of predator-prey interactions- What are the ecological effects of anti-predation decision making? *Bioscience* **48**, 25-34.
- Lima, S. L. (1998b). Stress and decision making under the risk of predation: recent developments from behavioural, reproductive and ecological perspectives. *Advances in the Study of Behaviour* **27**, 215-290.

- Lima, S. L. and Dill, L. M. (1990). Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619-640.
- Lima, S. L., Zollner, P. A., and Bednekoff, P. A. (1999). Predation, scramble competition, and the vigilance group size effect in dark-eyed juncos (*Junco hyemalis*). *Behavioural Ecology and Sociobiology* **46**, 110-116.
- Lind, J. (2004). What determines probability of surviving predator attacks in bird migration?: the relative importance of vigilance and fuel load. *Journal of Theoretical Biology* **231**, 223-227.
- Lind, J. and Cresswell, W. (2005). Determining the fitness consequences of anti-predation behaviour. *Behavioral Ecology* **16**, 945-956.
- Maclean, I. D., Austin, G. E., Rehfish, M. M., Blew, J., Crowe, O., Delany, S., Devos, K., Deceuninck, B., Gunther, K., Laursen, K., Van Roomen, M., and Wahl, J. (2008). Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Global Change Biology* **14**, 2489-2500.
- McNamara, J. (1982). Optimal patch use in a stochastic environment. *Theoretical Population Biology* **21**, 269-285.
- McNamara, J. M. and Houston, A. I. (1994). The effect of a change in foraging options on intake rate and predation rate. *American Naturalist* **144**, 978-1000.
- Pan, W. (2001). Akaike's Information Criterion in Generalized Estimating Equations. *Biometrics* **57**, 120-125.
- Pederson, M. B. (1995). Opportunistic behaviour as key-determinant in the winter strategy of the Jack Snipe *Limnocryptes minimus* in southern Scandinavia. *Wader Study Group Bulletin* **78**, 23-26.
- Pomeroy, A. C. (2006). Tradeoffs between food abundance and predation danger in spatial usage of stopover site by western sandpipers, *Calidris mauri*. *Oikos* **112**, 629-637.

- Pomeroy, A. C., Acevedo Seaman, D. A., Butler, R. W., Elner, R. W., Williams, T. D., and Ydenberg, R. C. (2008). Feeding-Danger Trade-Offs Underlie Stopover Site Selection by Migrants. *Avian Conservation and Ecology* **3**, 7.
- Rehfish, M. M., Clark, N. A., Langston, R. H. W., and Greenwood, J. J. D. (1996). A Guide to the Provision of Refuges for Waders: An Analysis of 30 Years of Ringing Data from the Wash, England. *Journal of Applied Ecology* **33**, 673-687.
- Rehfish, M. M., Insley, H., and Swann, B. (2003). Fidelity of overwintering shorbirds to roosts on the Moray Basin, Scotland: Implications for prediction impacts of habitat loss. *Ardea* **91**, 53-70.
- Rochette, R. and Dill, L. M. (2000). Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. *Journal of Experimental Marine Biology and Ecology* **263**, 165-191.
- Sansom, A., Lind, J., and Cresswell, W. (2009). Individual behavior and survival: the roles of predator avoidance, foraging success and vigilance. *Behavioral Ecology* **In Press**.
- Sparrevik, E. and Leonardsson, K. (1995). Effects of large *Saduria entomon* (Isopoda) on spatial distribution of their small *S.entomon* and *Monoporeia affinis* (Amphipoda) prey. *Oecologia* **101**, 177-184.
- Symonds, F. L. and Langslow, D. R. (1984). Movements of Winter Shorebirds withing the Firth of Forth: Species Differences in Usage of an Intertidal Complex. *Biological Conservation* **28**, 187-215.
- Todd, I. A. and Cowie, R. J. (1990). Measuring the risk of predation in an energy currency: field experiments with foraging blue tits *Parus caeruleus*. *Animal Behaviour* **40**, 112-117.
- Warnock, N., Page, G. W., and Stenzel, L. E. (1995). Non-migratory movements of dunlins on their California wintering grounds. *Wilson Bulletin* **107**, 131-139.

Watkinson, A. R., Gill, J. A., and Hulme, M. (2004). Flying in the face of climate change: a review of climate change, past, present and future. *Ibis* **146**, 4-10.

Watts, B. D. (1991). Effects of predation risk on distribution within and between habitats in savannah sparrows. *Ecology* **72**, 1515-1519.

Whitfield, D. P. (1985). Raptor predation on wintering waders in southeast Scotland. *Ibis* **127**, 544-548.

Whitfield, D. P. (2003). Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk *Accipiter nisus* predation. *Journal of Avian Biology* **34**, 163-169.

Whittingham, M. J. and Evans, K. L. (2004). The effects of habitat structure on predation risk in birds in agricultural landscapes. *Ibis* **146 supplement 2**, 210-220.

Yasué, M., Quinn, J. L., and Cresswell, W. (2003). Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in redshanks. *Functional Ecology* **17**, 727-736.

CHAPTER 6: DISCUSSION

REDSHANKS AS A CASE STUDY OF THE PREDATION-STARVATION RISK TRADE-OFF

The trade-off between starvation risk and predation risk often occurs because animals are unable to meet their energy requirements in a safe foraging environment or without attracting the attention of potential predators (Lima and Dill 1990).

Redshanks (*Tringa totanus*) overwintering in temperate countries such as the UK are vulnerable to mortality from starvation through severe cold weather and also habitat loss (Davidson and Evans 1982; Clark 1982; Insley *et al.* 1997; Burton *et al.* 2006). This vulnerability to starvation can then sometimes lead to redshanks making foraging decisions that increase predation risk, leading to mortality or other fitness consequences caused by predation (Cresswell and Whitfield 2008). Conversely predation risk also has non-lethal effects on redshanks, causing them to feed in less profitable areas away from risk (for example Cresswell 1994a). Given that redshanks must often contend with both exposure to predators and risk of starvation during the winter and that the two often interact, the behaviour of overwintering redshanks provides an ideal case study of the starvation predation risk trade-off.

Overwintering redshanks are generally site faithful (Burton 2000; Rehfishch *et al.* 1996; Rehfishch *et al.* 2003), which to some extent limits the spatial flexibility of any response to increased starvation or predation risk. For example redshanks are unlikely to move hundreds or thousands of kilometres to new foraging areas within a winter even if starvation risk increases dramatically in cold weather. However, within the spatial and temporal scale in which they operate redshanks show a wide variety of responses to predation and starvation risk, these act along the whole of the attack-avoidance continuum, ranging from choice of foraging area to behavioural mitigation against risk of capture when attacked, examples of which are given in Table 6.1 and are discussed in more detail.

Table 6.1. Some examples of studies on redshanks that specifically look at the effect of predation risk and anti-predation behaviour, showing where they are relevant along different stages along the avoidance-capture reducing continuum, and showing how anti-predation behaviour acts at different spatial scales.

Point at which risk is reduced	Evidence for behaviour/ selection	Chapter number/ Reference
Foraging under risk attack by predators	Redshanks use predator specific escape strategies, which increase chance of escape when attacked	(Cresswell 1993)
	Alarm calls function more to inform other conspecifics of predator presence rather than to coordinate escape responses, so potentially reducing long term predator success rate within an area and so predator density	(Cresswell 1994c)
	Escape delay when attacked varies within flocks, with vigilant, tightly spaced individuals and those closest to the attacking predator (sparrowhawk) flying most quickly, suggesting risk varies within flocks.	(Hilton <i>et al.</i> 1999a)
	Individuals that respond first to an 'attack' have longer escape delay times in larger flocks, and when stimulus is harmless; secondary individuals have longer delays when flocks are widely spaced. Suggests flocks reduce risk by dilution and confusion, and that variation in delays are caused by variation in risk and perceptual limitations.	(Quinn and Cresswell 2005)
	Risk of predation from sparrowhawks causes redshanks to abandon territories.	(Whitfield 1988)
	Sparrowhawks are more likely to target individuals that are further from their nearest neighbour. Flocks are more tightly spaced on edge most likely to be attacked. Suggests spacing within flocks affect individual risk of predation ('selfish herd' effect).	(Quinn and Cresswell 2006)
	Competition within flocks increases flock spacing and activity which increases vulnerability to predation from sparrowhawks	(Minderman <i>et al.</i> 2006)

	Foraging in a larger flock decreases risk of predation by sparrowhawks through dilution, vigilance effects and the confusion effect	(Cresswell 1994c)
	Individual intake rates are not constrained by competition (due to decrease in time spent on vigilance) allowing large flocks to form	Chapter 2, (Sansom <i>et al.</i> 2009)
	Sparrowhawks are more likely to attack smaller flocks	(Cresswell and Quinn 2004)
	When spending large amounts of time exposed to risk vigilance and intake rates increase survival time	Chapter 3 (Sansom <i>et al.</i> 2008)
	Sparrowhawks do not preferentially attack less vigilant individuals	(Cresswell <i>et al.</i> 2003)
	Increased distance from cover decreases the chance that an attack is successful	(Whitfield 2003b)
Foraging away from risk of attack	Redshanks avoid high risk areas where attack rates and risk of predation are high. Individuals only forage in high risk areas when forced to by competition (competitive ability) and environmental conditions (effect mainly in juveniles)	(Cresswell 1994a); (Hilton <i>et al.</i> 1999b); (Yasué <i>et al.</i> 2003);(Cresswell and Whitfield 2008)
	Individuals that spend less time exposed to high attack rate survive longer	Chapter 2 (Sansom <i>et al.</i> 2009)
	Mortality from predation is density dependant due to competition between foraging redshanks. Effects are stronger in juveniles who are probably forced to feed in higher risk areas.	(Whitfield 2003a)
	On rocky shores, regardless of risk, on the 100m scale, overwintering redshanks prefer the most profitable sites	Chapter 4
	Overwintering redshanks use more profitable sites in cold weather but do not have to increase their predation risk to do this	Chapter 5

AVOIDING ATTACK: BEHAVIOUR WHEN EXPOSED TO ATTACK

When animals cannot avoid exposure to risk of attack anti-predation behaviours are often used to reduce predation risk (in addition to spatial position). Redshanks use a wide variety of these behaviours, which again involve a trade-off between starvation and predation risk. One of the main ways in which risk is reduced for overwintering redshanks foraging under high risk of attack, again from sparrowhawks, is to feed in flocks (Cresswell 1994b). As flock size increases, competition also increases (Minderman *et al.* 2006; Selman and Goss-Custard 1988), however individuals are able to maintain their intake rates despite this due to a decrease in time spent vigilant (Sansom *et al.* 2008- chapter 2). This suggests that large groups can form reducing individual predation risk, but that eventually group-size will be limited by competition for food.

It is likely that risk of predation and the effects of competition will vary within groups, for example risk is likely to be higher on the side of the flock closest to predator concealing cover (Quinn and Cresswell 2006), and the effects of interference competition are likely to be greater and the 'back' edge of a flock, or for individuals closely spaced (Minderman *et al.* 2006). This means that the costs and benefits of being in a group will vary between individuals, especially because closer spacing reduces risk (Quinn and Cresswell 2006). Again this illustrates the importance of spatial aspects of the trade-off between starvation risk and anti-predator decision making; however, it is unclear exactly what role this plays in individual fitness because no strong effect of spacing, or position relative to cover has been found to affect individual survival (Sansom *et al.* 2009- chapter 3)- although not finding these effects this maybe an artefact of our small sample size. This may arise because spatial position and the trade-off between foraging success and safety within a group may affect fitness in other ways or reflect individual competitive ability. Alternatively, redshanks may be hunted by a variety of predators that use different methods (Cresswell 1993; Cresswell 1996) so that any position in the flock carries some degree of risk.

Vigilance is another anti-predation behaviour, which must often be traded-off with foraging (Lima 1998b). The role of vigilance in reducing predation risk in redshanks is not completely clear, it may act to increase survival through the early detection of

predators and early initiation of flight responses to predators, and/or to monitor the other individuals and their behaviour in response to potential threats. Additionally vigilant individuals may avoid costly flight responses to harmless stimuli (Hilton *et al.* 1999a; Quinn and Cresswell 2005). Individuals that are able to spend more time being vigilant (possibly through higher foraging ability), when exposed often to attack have survive for longer (Sansom *et al.* 2009-chapter2). This may mean that vigilance can act to mitigate effectively against risk of predation. This might be especially true if risk is moderate and may allow individuals to forage in profitable areas, reducing starvation risk without greatly increasing their risk of predation. This might explain why overwintering redshanks do not always vary their choice of foraging site dependant on risk, and why profitable sites can be exploited throughout the winter as was found in chapter 4: compensation via vigilance may allow site specific risk to be moderated

CHOICE OF FORAGING LOCATION

Choosing where to feed is likely to have a large impact on many aspects of predation and starvation risk because both will vary between different habitat types and between different locations over large scales such as choice of over-wintering site and at a smaller scale such as locations within habitat patches and flocks. Redshanks forage across a wide variety of different habitats but generally show a preference for profitable, food rich and muddy substrates (Goss-Custard 1969; Yates *et al.* 1993; chapter 4). This is probably a reflection of the redshank's sensitivity to starvation risk. However habitat choice is often not purely based on profitability, but also on predation risk (Cresswell 1994a). The foraging decisions that redshanks make therefore illustrate the way in which animals spatially trade-off starvation risk with predation risk, the different scales over which this can occur, and the fact the risk of predation have 'non-lethal' effects on a system. As can be seen in Table 6.1, redshanks under predation risk from sparrowhawks (*Accipiter nisus*) avoid profitable but risky foraging areas and locations (for example Cresswell 1994a; Yasué *et al.* 2003; Whitfield 2003a; Hilton *et al.* 1999b) this shows that even when not directly exposed to attack redshank foraging decisions are influenced by predation risk. However, this foraging choice is affected by starvation risk, so that when weather is colder and energy budgets increase, individuals may forage more in areas where risk

of attack by predators is increased, so producing increased mortality from predation as an indirect effect of starvation risk (Cresswell and Whitfield 2008).

The spatial scale over which foraging decisions affect predation risk can be variable, larger scale decisions, where individuals forage away from risk of attack will obviously greatly affect survival. Chapter 3 of this thesis showed that individual variation in exposure to predation risk, probably due to variation in starvation risk, directly affects individual mortality from predation (Sansom *et al.* 2009). This provides evidence that there should be strong selection on attack avoidance, but also shows that despite this, starvation risk constrains animals to be exposed to risk of attack. This means that there is potential for individuals to reduce risk when closer to the point of attack and on a smaller spatial scale. For example redshanks reduce risk of predation by feeding further from predator concealing cover where attacks are less likely to be successful (Whitfield 2003b; Quinn and Cresswell 2004; and chapter 5). On even smaller scales redshanks can reduce their risk by their spacing and position within a flock (Quinn and Cresswell 2006); providing an illustration of the fact that redshanks, and other animals can spatially reduce risk at different points along the attack avoidance continuum.

The mechanism behind variation in exposure to predation risk can be the same across different spatial scales. For example at the Tynninghame estuary in Scotland, competition for safe foraging territories forces some individuals to move to forage on a risky habitat, where attacks are frequent and often successful (Cresswell 1994a); when on this habitat, on a smaller scale, competition also increases risk of predation as it causes flock spacing to increase (which increases individual risk) (Minderman *et al.* 2006; Quinn and Cresswell 2006). Competitive ability, and foraging are therefore likely to increase survival; acting at both these scales. Evidence, which suggests this is the case, is the finding that when spending large amounts of time foraging under risk of attack redshanks with high intake rates have longer survival times (Sansom *et al.* 2009-chapter 3). It is likely that competitive foraging ability will always be under strong selection because this will determine an individual's ability to avoid attack, and if this is not possible, how much time it can afford to allocate to anti-predation behaviours if under risk of attack (Cresswell 2003). In general population dynamics are affected greatly by variation in competitive foraging ability both theoretically

(Sutherland 1996) and empirically (Goss-Custard 1996).

OTHER FACTORS AFFECTING STARVATION AND PREDATION RISK

The role of predator behaviour

The role of predator hunting decisions, and hunting strategies is likely to also influence the fitness consequences of anti-predation decision making and affect the structuring of ecosystems (Lima 1998a; Lima 2002), however it is an area which has received less attention than the direct responses of prey to risk from predators. For redshanks it has been demonstrated that there is some interaction between redshank vulnerability and the hunting decisions that predators make. For example, sparrowhawks have been found to target smaller groups where they are more likely to make a successful attack (Cresswell and Quinn 2004). Additionally behaviours that affect redshank vulnerability, such as distance from cover, can be used to predict the hunting decisions of sparrowhawks (Quinn and Cresswell 2004). This illustrates the way in which behavioural decisions made by prey species will not only influence their probability of capture, but also the probability that they are attacked in the first place (even when foraging under predation risk). Further evidence of the interaction between predator hunting behaviour and prey behaviour from redshanks is that when frequently attacked by sparrowhawks (over the course of a day), redshanks respond to reduce risk at two spatial scales, by moving further from predator concealing cover, and also by moving entirely away from the areas where attack frequency is high (Hilton *et al.* 1999b). It is clear that both predator hunting behaviour and prey anti-predator responses can be flexible, which suggests there is potential for predator-prey 'arms races', with predator attempting to optimise their hunting success and prey attempting to reduce predation risk.

The roles of environmental conditions and population density

Variation in weather conditions can directly affect redshank mortality through risk of starvation (Clark 1982; Mitchell *et al.* 2000); and this is likely to affect habitat preferences and foraging decisions as discussed, with redshanks using profitable areas to over-winter. Variation in temperature is often the cause of temporal variation in starvation risk, which can also lead to variation in exposure to predation risk, indirectly affecting mortality (Cresswell and Whitfield 2008); also discussed above. However variation in weather can also have other affects on prey vulnerability, for

example, precipitation has been found to cause redshanks to forage more away from risk, and increase 'false' alarm flights, perhaps increasing risk by decreasing the effectiveness of predator detection (Hilton *et al.* 1999b). The role of wind speed and temperature might also be important in the trade-off between predation and starvation risk, again possibly affecting predator detection and increasing risk (Hilton *et al.* 1999b; Yasué *et al.* 2003).

As mentioned above competition can be the driving force behind foraging decisions, which affect predation risk. Increased competition can cause individuals to trade-off safety for food and vice-versa. Population density and competition effects are likely to interact with risk of starvation, habitat availability and environmental conditions to affect risk of predation (Yates *et al.* 2000; Minderman *et al.* 2006; Cresswell 1994a; Yasué *et al.* 2003; Sansom *et al.* 2009). Population density effects can therefore directly affect predator hunting success, when population density is high and there is competition for 'safe' foraging areas more individuals will be forced to forage under risk of predation and thus predators will have greater opportunities to attack successfully (Whitfield 2003a). Additionally high population density may also directly affect starvation risk, for example, in chapter 4, it was found that when the overwintering population reached its peak more individuals occupied areas that were less profitable. This could increase risk of starvation or indirectly affect predation risk if individuals have to reduce anti-predation behaviours to spend more time foraging. This also has implications for habitat loss, and suggests that overwintering redshanks need high-quality foraging habitats and/or areas where predation risk is lower to balance starvation risk with risk of predation (Burton *et al.* 2006;).

REDSHANK SYNTHESIS AND AREAS FOR FURTHER RESEARCH

It is clear that the trade-off between starvation risk and predation risk in redshanks is a complex interaction between the effects of habitat profitability, temperature (which affects starvation risk), other weather effects which affect predation risk, population density and intraspecific competition effects, the use of anti-predation behaviours, predator assemblage, predator hunting decisions, and the way in which habitat structure affects hunting success. These factors act over a variety of spatial scales and also vary over time. This complex picture is a reflection of the fact that the effect of

predation on foraging decision in animals goes far beyond direct interactions between predators and prey (Lima 1998a; Cresswell 2008; Sih *et al.* 2006; Lima 2002).

Much is known about the effects of sparrowhawk predation on the foraging decisions made by redshanks (see examples in Table 6.1). However, other predators are responsible for winter mortality in redshanks, such as merlins (*Falco columbarius*) and peregrine falcons (*Falco peregrinus*), (Cresswell and Whitfield 1994; Cresswell 1993). The extent to which sparrowhawk predation regulates redshank behaviour and choice of foraging location, and winter mortality is likely to be limited by the occurrence of specific situations where highly profitable foraging areas occur close to cover, and where competition for safe areas and the effects of temperature on starvation force individuals to use these areas, allowing for successful attacks (Cresswell 1994a; Whitfield 2003b; Whitfield 2003a).

Predation risk posed by peregrine falcons is like to occur more frequently across different situations and in different areas, and is also therefore likely to strongly affect the foraging decisions made by redshanks overwintering on British estuaries. If redshanks are mainly exposed to risk of predation by peregrine falcons when overwintering it may be that selection has geared their anti-predation behaviours towards this threat. This could mean that behavioural responses to the threat posed by sparrowhawks are 'sub-optimal', explaining why mortality is so high when redshanks are exposed to this predator (Cresswell and Whitfield 1994).

If redshanks avoid areas with large amounts of cover, and prefer areas where they can forage further from cover, this suggests that for redshanks there may be a general 'rule of thumb' whereby feeding away from cover reduces risk from multiple raptor species. It would be interesting to know the extent to which foraging decisions relating to predation risk can reduce risk, from multiple predators in a general way, and the extent to which predator specific behaviours are relied upon; and the relative role of, and strength of selection on such general and specific responses.

Given that temperature has a strong influence on starvation risk and the trade-off between starvation and predation risk in redshanks (Davidson and Evans 1982; Cresswell and Whitfield 2008), redshanks make an interesting study species to

investigate what effects climate change might have on predator-prey interactions. If cold weather during the winter becomes less common (Watkinson *et al.* 2004), the choices that overwintering redshanks make may become less dependant of reducing risk of starvation and more dependant on other factors, such as predation risk and competition. It may mean that over a variety of spatial scales redshanks forage to reduce risk and/or competition, whilst meeting their energy budget rather than having to increase their level of risk to maximise intake. Given that predator hunting behaviour is likely to be flexible, any shifts in the distribution of prey species in relation to predation risk are likely to be followed by alterations in predator hunting activities (Lima 2002). Therefore climate change might have important implications for the distribution of both predators and prey and selection pressure on different anti-predator behaviours, and predator hunting behaviours. Greater understanding of the way in which predators respond to changes in the vulnerability of prey species will increase our knowledge of the effect climate change, habitat loss and changes in distributions will have on whole ecosystems, not only in redshanks but across other species groups.

GENERAL SYNTHESIS

The results of this thesis, and the long term redshank study, can probably be generalised to many other prey species. There are a number of general points that probably apply to all systems in which behaviourally complex prey are hunted by behaviourally complex predators over a variable spatial and temporal scale:

1. The way in which predators and prey interact should determine the type of behaviours which prey use to avoid predation and the behaviours which predators use to optimise their hunting success (Endler 1991; Lima and Zollner 1996). When anti-predation behaviours, which reduce the risk of attack are costly then animals should employ such behaviours, only when the threat posed from predators is high (Lima and Bednekoff 1999). Conversely when animals are able to avoid risk and do not interact with predators this does not mean that selection on avoidance becomes weak, because there will still be a high cost to fitness when avoidance fails (Brodie and Formanowicz 1991).
2. The spatial scales over which predators and prey interact are likely to be variable, as are the scales over which avoidance and capture reducing behaviours operate, but on both large and small scales, selection pressures act on both predator

hunting behaviours and prey anti-predation behaviours. For example when animals use refuges they avoid predators on a small spatial scale, the prey must then make decisions about when to leave a refuge, and a potential predator must decide how long to wait for the prey to do this. For the prey the consequence of making the 'wrong' decision is likely to be death, whereas for the predator it is loss of a meal, leading to different selection pressures on predators and prey in this 'game' (Hugie 2004). On a larger spatial scale prey vulnerability and predator hunting success can be influenced by or interact with the structure of the environment (Whittingham and Evans 2004).

3. In a similar way temporal variation in risk can influence the foraging decisions made by prey and predators. For example if risk is greater during day-time, this can lead to the evolution of prey that are nocturnal and predators which then evolve to specialise to hunt such prey (Rydell and Speakman 1995). On a different time scale the timing of migration of prey animals can be greatly affected by temporal variation in predation risk (Alerstam and Lindstrom 1990).
4. The capacity for prey animals to compensate for predation risk by forming a group has implications for prey foraging decisions, and for predator hunting strategies and success (Krause and Ruxton 2002). The tendency of animals to form groups or the size of group that is formed is affected by several factors, for example:
 - a. Interference competition within groups, and its effect on intake rates may limit the size of group that can be formed, and therefore limit a group's effectiveness as a defence against predation (Beauchamp 1998). It also affects individual decisions regarding when to leave or join a group, meaning that energetic state, or individual competitive ability can indirectly affect an individual's predation risk (Livoreil and Giraldeau 1997).
 - b. Population density can also limit the size of groups which can be formed, if populations are small or fragmented, then groups that are optimal in size - in terms of the trade-off between vigilance and foraging - may not be possible, this might exacerbate the problems facing rare or endangered animals by increasing their mortality through predation (for example (Watson *et al.* 2007). Conversely when suitable habitat is limited and population density is high, larger groups may form, increasing predation risk (for example Hebblewhite and Pletscher 2002).

- c. Ecological conditions might affect whether or not a group is formed or the size of a group, for example in teal (*Anas crecca*), as the quality of a foraging patch increases so does the size of the group formed (Pöysä 1991). The use of groups is also likely to be affected by the way in which risk interacts with habitat structure, for example animals might only feed far from protective cover if in a large group (for example Wahungu *et al.* 2001).
5. The importance of predator hunting decisions and tactics is key to understanding predator-prey dynamics, and the way in which selection acts on anti-predator behaviours (Lima 2002). Additionally the make up of the predator community in an area can have non-additive effects on predation risk, and on behavioural responses to risk. For example if different predator species have different hunting tactics and the most appropriate response to one type of predator increases vulnerability to another then selection may act only on the behaviour which reduces risk from the most abundant predator, or may result in prey which are not adapted to respond 'optimally' to either predator (Sih *et al.* 2006).

REFERENCES

- Alerstam, T. and Lindstrom, A. (1990). Optimal bird migration: the relative importance of time, energy and safety. In 'Bird Migration: physiology and ecophysiology.' (Ed E. Gwinner.) pp. 331-351. (Springer-Verlag: Berlin.)
- Beauchamp, G. (1998). The effect of group size on mean food intake rate in birds. *Biological Reviews of the Cambridge Philosophical Society* **73**, 449-472.
- Brodie, E. D. and Formanowicz, D. R. (1991). Predator avoidance and antipredator mechanisms - distinct pathways to survival. *Ethology Ecology & Evolution* **3**, 73-77.
- Burton, N. H. K. (2000). Winter site-fidelity and survival of Redshank *Tringa totanus* at Cardiff, south Wales. *Bird Study* **47**, 102-112.
- Burton, N. H. K., Rehfisch, M. M., Clark, N. A., and Dodd, S. G. (2006). Impacts of sudden winter habitat loss on the body condition and survival of redshank *Tringa totanus*. *Journal of Applied Ecology* **43**, 464-473.

- Clark, N. A. (1982). The effects of severe weather in December 1981 and January 1982 on waders in Britain. *Wader Study Group Bulletin* **34**, 5-7.
- Cresswell, W. (1993). Escape responses by redshanks, *Tringa totanus*, on attack by avian predators. *Animal Behaviour* **46**, 609-611.
- Cresswell, W. (1994a). Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *Journal of Animal Ecology* **63**, 589-600.
- Cresswell, W. (1994b). Flocking is an effective anti-predation strategy in Redshanks, *Tringa totanus*. *Animal Behaviour* **47**, 433-442.
- Cresswell, W. (1994c). The function of alarm calls in redshanks, *Tringa totanus*. *Animal Behaviour* **47**, 736-738.
- Cresswell, W. (1996). Surprise as a winter hunting strategy in Sparrowhawks *Accipiter nisus*, Peregrines *Falco peregrinus* and Merlins *F. columbarius*. *Ibis* **138**, 684-692.
- Cresswell, W. (2003). Testing the mass-dependent predation hypothesis: in European blackbirds poor foragers have higher overwinter body reserves. *Animal Behaviour* **65**, 1035-1044.
- Cresswell, W. (2008). Non-lethal effects of predation in birds. *Ibis* **150**, 3-17.
- Cresswell, W., Lind, J., Kaby, U., Quinn, J. L., and Jakobsson, S. (2003). Does an opportunistic predator preferentially attack non-vigilant prey? *Animal Behaviour* **66**, 643-648.
- Cresswell, W. and Quinn, J. L. (2004). Faced with a choice, predators select the most vulnerable group: implications for both predators and prey for monitoring relative vulnerability. *Oikos* **104**, 71-76.

Cresswell, W. and Whitfield, D. P. (1994). The effects of raptor predation on wintering wader populations at the Tynninghame estuary, southeast Scotland. *Ibis* **136**, 223-232.

Cresswell, W. and Whitfield, D. P. (2008). How starvation risk in Redshanks *Tringa totanus* results in predation mortality from Sparrowhawks *Accipiter nisus*. *Ibis* **150**, 209-218.

Davidson, N. C. and Evans, P. R. (1982). Mortality of redshank and oystercatchers from starvation during severe weather. *Bird Study* **29**, 183-188.

Endler, J. A. (1991). Interactions between predators and prey. In 'Behavioural Ecology: An Evolutionary Approach.' (Eds J. R. Krebs and N. B. Davies.) pp. 169-196. (Blackwell: Oxford.)

Goss-Custard, J. D. (1969). The winter feeding ecology of the redshank *Tringa totanus*. *Ibis* **111**, 338-356.

Goss-Custard, J. D. (1996). 'The Oystercatcher: from individuals to populations.' (Oxford University Press: Oxford.)

Hebblewhite, M. and Pletscher, D. (2002). Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* **80**, 800-809.

Hilton, G. M., Cresswell, W., and Ruxton, G. D. (1999a). Intra-flock variation in the speed of response on attack by an avian predator. *Behavioral Ecology* **10**, 391-395.

Hilton, G. M., Ruxton, G. D., and Cresswell, W. (1999b). Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. *Oikos* **87**, 295-302.

Hugie, D. M. (2004). The waiting game: a "battle of waits" between predator and prey. *Behavioral Ecology* **14**, 807-817.

- Insley, H., Peach, W., Swann, B., and Etheridge, B. (1997). Survival rates of Redshank *Tringa totanus* wintering on the Moray Firth. *Bird Study* **44**, 277-289.
- Krause, J. and Ruxton, G. D. (2002). 'Living in groups.' (Oxford University Press: Oxford.)
- Lima, S. L. (1998a). Nonlethal effects in the ecological effects of predator-prey interactions- What are the ecological effects of anti-predation decision making? *Bioscience* **48**, 25-34.
- Lima, S. L. (1998b). Stress and decision making under the risk of predation: recent developments from behavioural, reproductive and ecological perspectives. *Advances in the Study of Behaviour* **27**, 215-290.
- Lima, S. L. (2002). Putting predators back into behavioral predator-prey interactions. *Trends in Ecology and Evolution* **17**, 70-75.
- Lima, S. L. and Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist* **153**, 649-659.
- Lima, S. L. and Dill, L. M. (1990). Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619-640.
- Lima, S. L. and Zollner, P. A. (1996). Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* **11**, 131-135.
- Livoreil, B. and Giraldeau, L.-A. (1997). Patch departure decisions by spice finches foraging singly or in groups. *Animal Behaviour* **54**, 967-977.
- Minderman, J., Lind, J., and Cresswell, W. (2006). Behaviourally mediated indirect effects: interference competition increases predation mortality in foraging redshanks. *Journal of Animal Ecology* **75**, 713-723.

Mitchell, P. I., Scott, I., and Evans, P. R. (2000). Vulnerability to severe weather and regulation of body mass of Icelandic and British Redshank *Tringa totanus*. *Journal of Avian Biology* **31**, 511-521.

Pöysä, H. (1991). Effects of predation risk and patch quality on the formation and attractiveness of foraging groups of teal, *Anas crecca*. *Animal Behaviour* **41**, 285-294.

Quinn, J. L. and Cresswell, W. (2004). Predator hunting behaviour and prey vulnerability. *Journal of Animal Ecology* **73**, 143-154.

Quinn, J. L. and Cresswell, W. (2005). Escape response delays in wintering redshank, *Tringa totanus*, flocks: perceptual limits and economic decisions. *Animal Behaviour* **69**, 1285-1292.

Quinn, J. L. and Cresswell, W. (2006). Testing for domains of danger in the selfish herd: sparrowhawks target widely spaced redshanks in flocks. *Proceedings of the Royal Society of London Series B* **273**, 2521-2526.

Rehfish, M. M., Clark, N. A., Langston, R. H. W., and Greenwood, J. J. D. (1996). A Guide to the Provision of Refuges for Waders: An Analysis of 30 Years of Ringing Data from the Wash, England. *Journal of Applied Ecology* **33**, 673-687.

Rehfish, M. M., Insley, H., and Swann, B. (2003). Fidelity of overwintering shorebirds to roosts on the Moray Basin, Scotland: Implications for prediction impacts of habitat loss. *Ardea* **91**, 53-70.

Rydell, J. and Speakman, J. R. (1995). Evolution of nocturnality in bats: Potential competitors and predators during their early history. *Journal of the Linnean Society* **54**, 183-191.

Sansom, A., Cresswell, W., Minderman, J., and Lind, J. (2008). Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? *Animal Behaviour* **75**, 1869-1875.

Sansom, A., Lind, J., and Cresswell, W. (2009). Individual behavior and survival: the roles of predator avoidance, foraging success and vigilance. *Behavioral Ecology* **In Press**.

Selman, J. and Goss-Custard, J. D. (1988). Interference between foraging redshanks *Tringa totanus*. *Animal Behaviour* **36**, 1542-1544.

Sih, A., Englund, G., and Wooster, D. (2006). Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* **13**, 350-355.

Sutherland, W. J. (1996). 'From individual behaviour to population ecology.' (Oxford University Press: Oxford.)

Wahungu, G. M., Catterall, C. P., and Olsen, M. F. (2001). Predator avoidance, feeding and habitat use in the red-necked pademelon, *Thylogale thetis*, at rainforest edges. *Australian Journal of Zoology* **49**, 45-58.

Watkinson, A. R., Gill, J. A., and Hulme, M. (2004). Flying in the face of climate change: a review of climate change, past, present and future. *Ibis* **146**, 4-10.

Watson, M., Aebischer, N. J., and Cresswell, W. (2007). Vigilance and fitness in grey partridges *Perdix perdix* :the effects of group size and foraging-vigilance trade-offs on predation mortality. *Journal of Animal Ecology* **76**, 211-221.

Whitfield, D. P. (1988). Sparrowhawks *Accipiter nisus* affect the spacing behaviour of wintering Turnstone *Arenaria interpres* and Redshank *Tringa totanus* . *Ibis* **130**, 284-287.

Whitfield, D. P. (2003a). Predation by Eurasian sparrowhawks produces density-dependent mortality of wintering redshanks. *Journal of Animal Ecology* **72**, 27-35.

Whitfield, D. P. (2003b). Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk *Accipiter nisus* predation. *Journal of Avian Biology* **34**, 163-169.

Whittingham, M. J. and Evans, K. L. (2004). The effects of habitat structure on predation risk in birds in agricultural landscapes. *Ibis* **146 supplement 2**, 210-220.

Yasué, M., Quinn, J. L., and Cresswell, W. (2003). Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in redshanks. *Functional Ecology* **17**, 727-736.

Yates, M. G., Goss-Custard, J. D., Mcgrorty, S., Lakhani, K. H., Durell, S. E. A. L., Clarke, R. T., Rispin, W. E., Moy, I., Yates, T., Plant, R. A., and Frost, A. J. (1993). Sediment characteristics, invertebrate densities and shorebirds densities on the inner banks of the Wash. *Journal of Applied Ecology* **30**, 599-614.

Yates, M. G., Stillman, R. A., and Goss-Custard, J. D. (2000). Contrasting interference functions and foraging dispersion in two species of shorebird (Charadrii). *Journal of Animal Ecology* **69**, 314-322.

APPENDIX 1:

Weather data for the 12 years covered by the WeBS counts in Chapter 5

Table 1. Total number of frost days in each winter year

Year	Frost days per Winter
1994	29
1995	29
1996	35
1997	16
1998	28
1999	28
2000	39
2001	29
2002	29
2003	35
2004	34
2005	37

Table 2. Mean Matched minimum temperatures for each month of each year, showing standard errors, and number of frost days in each month.

Year	Month	Mean Matched Minimum Temperature (°C)	Standard Error of the Mean	Frost days
1994	November	7.66	0.17	0
	December	3.58	0.27	8
	January	1.61	0.18	14
	February	0.99	0.21	7
1995	November	1.23	0.51	2
	December	-0.68	0.37	13
	January	4.08	0.23	3
	February	3.05	0.19	13
1996	November	0.87	0.21	12
	December	-0.30	0.56	9
	January	1.22	0.16	9
	February	2.63	0.22	5
1997	November	2.98	0.35	0
	December	1.62	0.22	5
	January	6.29	0.49	9
	February	5.91	0.54	2
1998	November	3.47	0.42	5
	December	3.43	0.33	8
	January	3.41	0.59	6
	February	1.51	0.26	9
1999	November	1.57	0.50	3
	December	-0.78	0.35	12
	January	0.65	0.13	7

	February	0.28	0.27	6
2000	November	3.52	0.19	1
	December	5.30	0.55	13
	January	0.34	0.28	12
	February	-0.54	0.30	13
2001	November	6.11	0.52	2
	December	1.69	0.39	16
	January	2.88	0.23	8
	February	3.54	0.20	3
2002	November	3.61	0.47	0
	December	2.08	0.83	5
	January	3.50	0.62	12
	February	-2.22	0.48	12
2003	November	5.06	0.59	3
	December	2.39	0.27	11
	January	2.41	0.44	10
	February	0.18	0.24	11
2004	November	-2.07	0.92	9
	December	3.91	0.21	11
	January	3.97	0.15	6
	February	3.30	0.23	8
2005	November	2.49	0.47	10
	December	4.63	0.26	13
	January	4.47	0.23	8
	February	0.05	0.25	6