STRUGGLE FOR SAFETY

Adaptive responses of wintering waders to their avian predators

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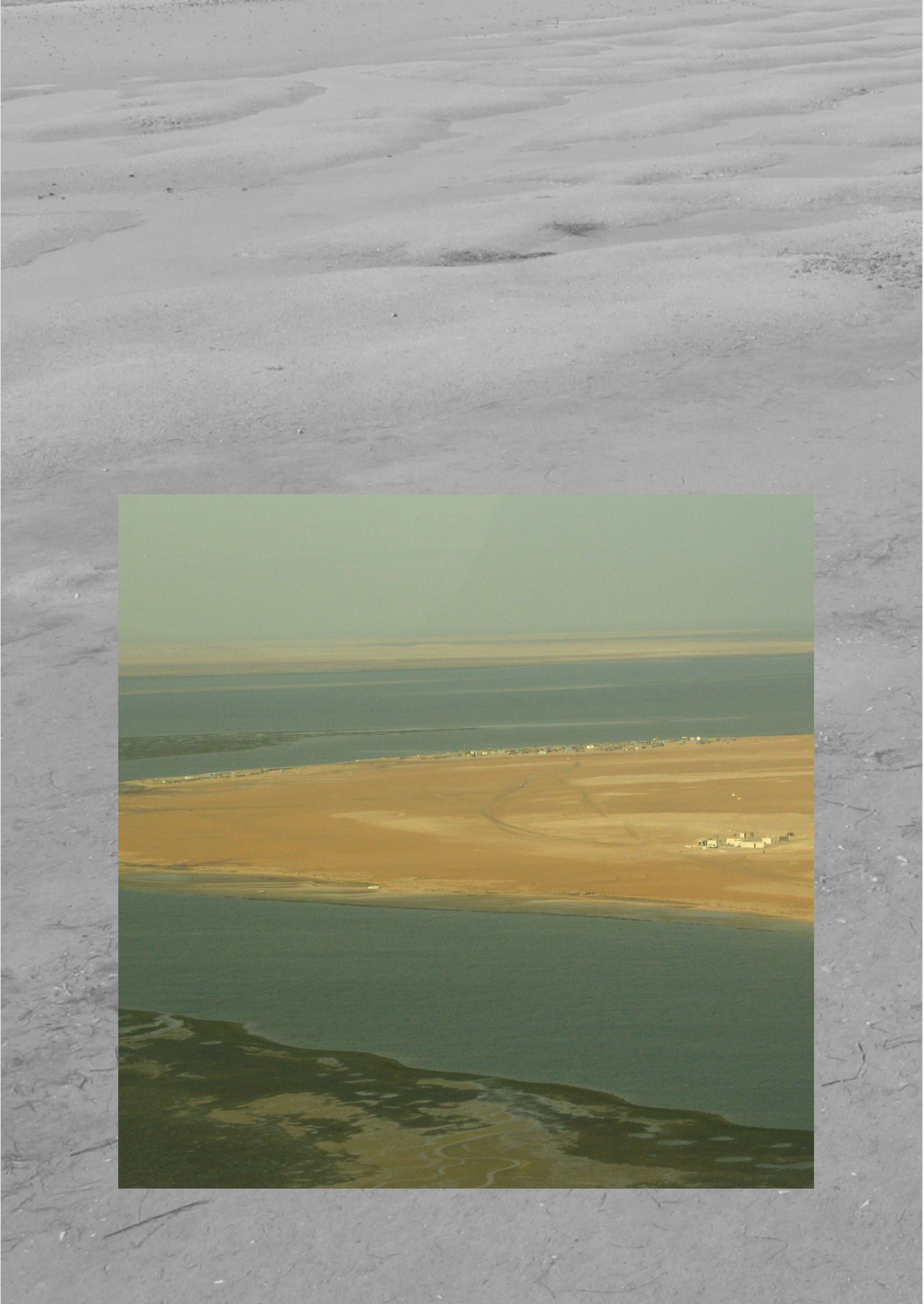
PART I

PREAMBLE



CHAPTER 1

General Introduction

Piet J. van den Hout

Explaining why this thesis was written – and casting a glance at last century's achievements in predation studies – then explaining why risk differs from danger – subsequently introducing the study system that yielded this thesis – and finally revealing the topics that were studied and conveying how the chapters unfold the stories.

MOTIVATION FOR THIS THESIS

As yet, the vast majority of shorebird studies have focused on shorebirds as predators of worms, bivalves, gastropods, shrimps and their likes (see van de Kam *et al.* 2004 for an extensive summary). Only a minority of studies focused on the role of shorebirds as potential prey for higher trophic levels. This is understandable, as attacks on shorebirds are rarely witnessed, whereas foraging shorebirds can readily be observed. Yet, as shorebirds can only benefit from foraging if they avoid becoming food themselves, their ecology cannot be fully understood without an understanding of predation costs. Although the issue of shorebird predation has been quite well integrated into foraging ecology, a lot of questions still remain. For example, with respect to the consumptive effects of predators on shorebirds (how many are killed?), differential vulnerabilities of classes of birds (which individuals are most vulnerable and why?), and the various – behavioural, morphological and physiological – ways in which shorebirds manage predation danger. All of this converges on the question what the costs of predation are for shorebirds, and how and why they vary. In this thesis, with respect to non-breeding shorebirds, I aim to shed more light on these questions.

In Collins Dictionary of the English Language predation is defined as "a relationship between two species of animal in a community, in which one (the predator) hunts, kills, and eats the other (the prey)". Likewise, in this thesis we regard predation as a special kind of consumption, next to other kinds of consumption, like herbivory and detrivory (Yodzis 1989). Predators can affect prey through basically two mechanisms: (1) via the killing of individuals and (2) through eliciting behavioural responses in prey (anti-predation defences). As the first (obviously) affects prey fitness directly, the second affects fitness through missed opportunities for survival or reproduction (Cresswell 2008).

Due to prey responsiveness, death rates do not increase in direct proportion with an increase in predator numbers (Abrams 1993). Therefore, for a proper understanding of predatory impact on prey populations prey responsiveness to predation must be taken into account.

Prey, in turn, also influence the behaviour of predators. In fact, predator-prey interactions involve two opposing selection pressures as the predator's ability to catch and kill prey is counteracted by the prey's ability to avoid predation. Yet, this interaction is asymmetric, as an individual prey has more to lose by failure to avoid a predator, than predators by failing to catch a prey (Dawkins 1999). For this reason, selection pressure on anti-predation measures must be very strong, which underpins the pivotal role of predation in behavioral ecology (Lima & Dill 1990).

A BRIEF HISTORY OF PREDATION STUDIES

Ever since predation became subject of study it has been studied from a great variety of view-points. Starting in the 1940s, studies of predation focused primarily on the consumptive side of predation, questioning whether predators are capable of regulating prey populations by killing prey (Errington 1946a, 1946b, Tinbergen 1946, Pearson & Pearson 1947). Leopold's idea, proposed in the 1940s, that top-predators are a necessary component of all ecosystems and that their loss can eventually lead to severe reductions in carrying capacity of the environment (Leopold 1943, Leopold *et al.* 1947), was influential for a decade or two. But it dissolved after having been thoroughly contested (Caughly 1970); as later appeared, unjustifiably (Ripple & Beschta 2005).

Meanwhile attention was given to hunting styles and prey selectivity by raptors (Rudebeck 1950-1951). Yet, such time-consuming field studies remained scarce until Dekker started up his intensive studies of foraging habits and capture rates of four species of bird-hunting falcons from the 1980s onward (Dekker 1980, 1985, 1988, 1995, 1998, 2003, Dekker & Lange 2001, Dekker & Court 2003, Dekker & Ydenberg 2004, Dekker & Taylor 2005).

It has taken some time, however, for predation to become an integral part of foraging ecology (Bednekoff 2007). Several studies in the early 1980s pointed at the pervasive effects of predation danger on foraging (Dill & Fraser 1984, Kotler 1984). The influential textbook *Foraging Theory* by Stephens and Krebs (1986) casually touched upon trade-offs between energy gain and safety, mentioning a single study by Lima *et al.* (1985). But the flood of studies that included costly anti-predation measures in response to predation danger discharged from mid 1980s onward, culminating in the first important review in 1990 by Lima and Dill, and its follow-up by Lima in 1998. Meanwhile the study of behavioural interactions between predator and prey had greatly increased understanding of prey behaviour, such that is became clear that nearly any aspect of prey decision-making can be affected by predation danger. At the end of the 1980s two new tools started to make it possible to titrate the balanced interests of food and safety. Firstly, the way of expressing energy gain and safety from predators into a common currency (Abrahams & Dill 1989); secondly, the concept of giving-up densities (GUDs) in depletable food patches and the distribution of foragers across safe and risky feeding opportunities (Brown 1988). Complying with Lima's appeal not to engage one-sidedly in prey-responsiveness, but likewise recognizing responsiveness of predators to prey (Lima 2002), a great number of detailed field studies on predator-prey interactions have complemented these experiments (reviewed in Cresswell 2008).

To make the prey's and predators' opposing selection pressures workable in a population ecological context, Brown *et al.* (1999) introduced the 'Ecology of Fear'. This included the concept of fear-driven ("μ-driven") population interactions as opposed to mortality-driven ("N-driven") interactions (Box II). These ideas were closely linked to the asset-protection principle as introduced by Clark (1994), stating that the more an animal has to lose, the more fearful it should be.

The proceeding integration of predation into foraging theory went hand in hand with an increasing attention for the effects of predation on community dynamics, including the question how behaviour-mediated indirect effects of predation can affect community structure and coexistence between species (for a review see Kotler & Brown 2007).

Meanwhile predator-prey interactions have matured into a fully integrated part of foraging ecology. As expressed by Bednekoff (2007), danger is now treated as a matter of life and death, rather than just a distraction from rigorous experimental design.

MANAGING PREDATION

Lank and Ydenberg (2003) noticed the often ambivalent and indefinite use of the term 'predation risk', and proposed a clear distinction between predation risk and predation danger. They stated predation 'danger' to be essentially a theoretical concept, describing the probability of becoming prey if no anti-predation measures are taken. It refers to ecological properties of the environment such as the abundance of predators, the structure of the habitat, the availability of alternative prey (including conspecifics), and other factors that the prey cannot affect directly and quickly by its behaviour. Yet, as noted by Lima (2002), danger is rarely a fixed property of a certain location. It varies with time and place, for instance as predators adjust their hunting behaviour to the presence and behaviour of their prey. 'Predation risk', on the other hand, is the probability of getting killed by a predator, which can be controlled by the animal (Lima & Dill 1990, Lank & Ydenberg 2003) in a number of ways.

The most obvious way to control predation danger is to avoid predators, by hiding or by foraging in patches rarely visited by predators (Cresswell 2008). But, as said, particularly with mobile predators, complete avoidance is not often possible. As animals have to feed to avoid starvation, some exposure to danger is generally inevitable. As in many species morphological traits to avoid detection, such as crypsis, are not a sufficient defence against predation, these animals have to adjust the timing and places of their activities to prevalent levels of predation danger. For timely detection of predators, vigilance needs to be balanced with foraging. Yet, shared attentiveness may be gained by flocking, creating time for foraging. Flocking has several other anti-predation benefits such as risk dilution, and predator confusion (Krause & Ruxton 2002, Caro 2005), but it can also facilitate foraging by information transfer (Giraldeau 1997).

As appetizers to the main studies in this thesis, I present some casual observations illustrating two basic mechanisms which birds can adopt to control predation danger: flocking (CHAPTER 2) and vigilance (CHAPTER 3). The article about vigilance illustrates the possible caveats that are encountered when interpreting animal behaviour which is essentially an internal process that is not directly accessible to the senses of even the keenest observer.

STUDY SYSTEM

In this thesis we aim to shed more light on the impact predators may have on populations and individuals of coastal shorebirds in their non-breeding period. Controlled experiments at the Royal Netherlands Institute for Sea Research (NIOZ) were combined with field observations at Banc d'Arguin, Mauritania. Attempts to do observational and experimental studies closer to home were not as successful (Box I). The Banc d'Arguin is an area of shallow water and islands that stretches along the northern coast of Mauritania, bordering the Sahara desert (Fig. 1.1). It is the major wintering area for millions of shorebirds that breed in Arctic regions of Fenno-Scandia, Siberia, Greenland and Canada (Altenburg *et al.* 1982, Smit & Piersma, 1989, Zwarts *et al.* 1998a,b, Davidson & Stroud 2006). At Banc d'Arguin, shorebirds are hunted by migrant and resident raptor species, of which the large falcons (Box III) are most lethal. Prey remains (Fig. 1.2) were collected to assess the relative vulnerabilities of species and age-classes to predation by these large falcons. This information was complemented by observations on raptor-wader interactions. Colour-banding of shorebirds caught by mist nets allowed us to estimate survival, but also examine micro-habitat use (Fig. 1.3).

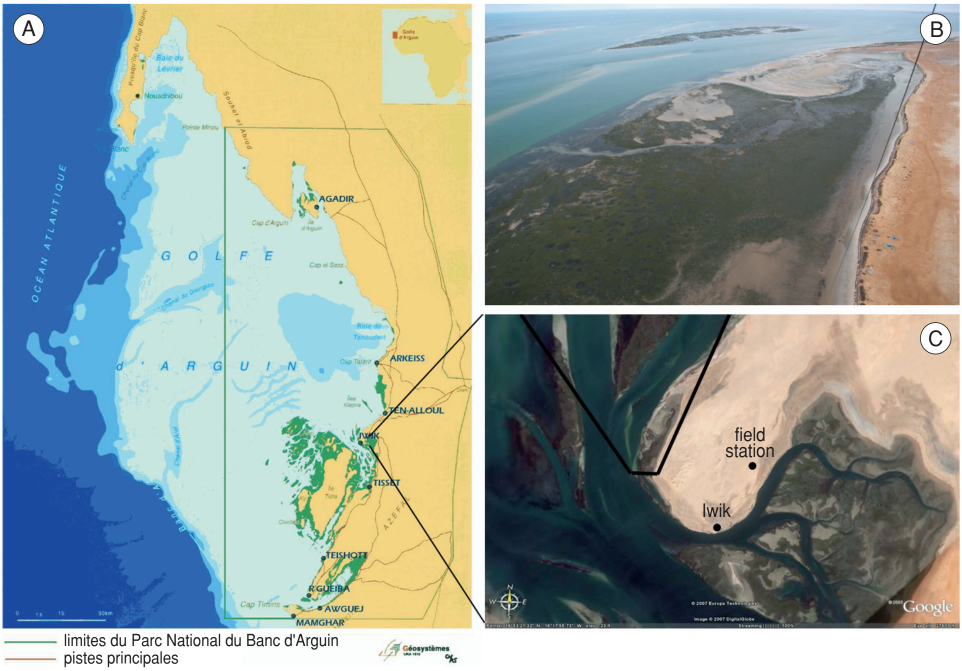


Figure 1.1 (A) The National Park of Banc d'Arguin in Mauritania at the border of the Sahara desert. (B) A bird eye view of a part of our study area (indicated by the angle shown in panel B), showing the transition between the desert and the intertidal mudflats, largely covered by seagrass (Photo courtesy by En Haut! M. Broquère - S. Nancy). (C) A closer (satellite) view of the study area of Iwik Peninsula and the surrounding mudflats. Green parts are seagrass beds (photo Google Earth).

LETHAL AND NON-LETHAL EFFECTS OF PREDATION

In Part II studies on lethal and non-lethal effects of predation are presented. In CHAPTER 4, for an array of wader species, we will examine to what extent direct mortality affects their wintering populations. Then for three species we estimate age-differences in predation mortality. Finally, for Red Knot *Calidris canutus*, we estimate the share of predation mortality in the local wintering population in view of all other causes of mortality, distinguishing between adult and juvenile birds.

The topic of age-differential impact of predation serves as a prelude for the discussion about how behaviours such as predator avoidance, foraging strategies and competitive foraging abilities may allow animals to manage predation danger and how trade-offs between energy gain and safety from predators may depend on factors such as energy state and individual abilities in foraging and competition (CHAPTER 5). The extent to which individual differences in such skills may affect patterns of distribution is discussed in CHAPTER 6.

FLEXIBLE ANTI-PREDATION ADJUSTMENTS IN BODY COMPOSITION

Apart from behaviour, which seems to be most flexible way to cope with changes in the environment, organisms may also demonstrate flexible adjustments in body composition. For instance, the digestive tract of many organisms responds rapidly and in highly integrated ways to variations in food quality and energy demand (Starck 2003, Battley 2005, Pennisi 2005, van Gils *et al.* 2005a). Furthermore, shorebirds were shown to go through rapid reversible changes in nearly all body parts before, during and after long-distance migration (Piersma & Lindström 1997). This includes the main flight organ of birds, the pectoral muscle complex, which demonstrates variability in a seasonal context (Marsh 1984, Evans *et al.* 1992, Jehl 1997,

Figure 1.2 Red Knot after being seized by a Lanner Falcon *Falco biarmicus* (photo Jeroen Reneerkens).

Figure 1.2 Colour-banding of birds and subsequent resightings enabled studies on demography and temporal and spatial patterns of habitat use.

Piersma *et al.* 1999), and was shown to increase in moulting birds in order to compensate for impaired flight ability (Lind & Jakobsson 2001).

In Part III such flexibility in body composition is investigated in a predation context. The prediction that shorebirds are capable of adjusting pectoral muscle or overall body mass to changing levels of predation danger is examined. In Chapter 7 this is tested in indoor experiments by exposing Ruddy Turnstones *Arenaria interpres* to a raptor model flying overhead and measuring changes in overall body mass and pectoral muscle size. In Chapter 8, in a similar indoor experimental set-up, but with Red Knots, we test the threat-sensitive predation-avoidance hypothesis, meaning that prey should match the intensity of their anti-predation response to the degree of threat posed by predators. In Chapter 9 the synergism between behaviour and morphology is underlined by discussing how escape tactics may differ between species depending on their foraging habits and related social behaviour, and wing morphology. We develop a theory based on aerodynamics to predict the most appropriate morphological responses to experimentally induced predation danger for two shorebird species that markedly differ in some of those aspects. Finally, in Part IV, our studies are discussed in a wider perspective including the role of falcons as top-predators in ecosystems that involve shorebirds as prey (Chapter 10).

Box I

Trial and Error

Why don’t you find as much ‘Wadden Sea’ in this thesis as you would perhaps have expected? It is not because no fieldwork was done in the Dutch Wadden Sea. Actually, quite some time and effort was spent on fieldwork here, and several colleagues, students and other volunteers participated in this. Although several student reports (by Jutta Leyrer, Jeroen Reimerink and Rob van Bemmelen) emerged from this field work, as yet Banc d’Arguin studies were given priority for scientific publications. Bringing together the results from our studies on raptor-shorebird relationships in the Wadden Sea has been deferred and not presented in this thesis. A short exposé of our study efforts should explain how this came about. It also illustrates the mistakes, the hooks and eyes, and other incidents that may accompany a research project, particularly in its early stages.

Just preceding this PhD-project, in August and September 2002, Jutta Leyrer (a trainee then and a colleague at present) and I set out to explore possible relationships between predation danger and several attributes of foraging, such as intake rates, flock size, inter-bird distance and time budgets. We started our activities on the mudflats surrounding the island of Griend in the western Wadden Sea (53°15′ N, 05°15′ E) where most of the studies on Red Knots in the Dutch Wadden Sea had been executed (e.g. Piersma *et al.*, 1993, Nebel *et al.*, 2000). At this point in time, with hindsight not surprisingly (Kraan *et al.*, 2009), we could hardly find any Red Knots. At most a few hundred individuals were spotted on the mudflats around Griend. At the same time, about 20 000 individuals were reported foraging on the mudflats surrounding the eastern part of the island of Schiermonnikoog (53°30′ N, 06°22′ E), in the eastern part of the Dutch Wadden Sea, so we moved to Schiermonnikoog. Although we were able to observe the Red Knots here, we were unable to connect these observations to measures of varying predation danger, for the simple reason that their main predator, the Peregrine Falcon *Falco peregrinus* was never observed on the offshore mudflats where we did our foraging observations. Peregrines were only now and then seen nearshore, particularly near the main shorebird roost (just as we later would observe at Banc d’Arguin – Chapter 4). In contrast to Red Knots in the Wadden Sea, Red Knots wintering at Banc d'Arguin turned out to be much more site-faithful with small home ranges (Leyrer *et al.*, 2006). This allowed for repeatable observations of individuals, and better opportunities to observe their interactions with the several falcon species that hunted them. In other words, the entire scenario of raptor-shorebird interactions unfolded itself in a relatively small area, which in winter appeared to be a virtually closed system. Prey remains were easier to find enabling calculations of relative vulnerabilities of species and age-classes. The large home ranges (Piersma *et al.* 1993, van Gils *et al.* 2006) and unpredictable appearance of shorebirds (and predators to a lesser extent) made it much more difficult to perform such investigations in the Wadden Sea. These differences made Banc d'Arguin a far more attractive site for this kind of fieldwork.

A year later, from 30 July –18 September 2003, we studied roost use of radiotagged Red Knots in the western Wadden Sea. Richel (53°25′ N, 05°35′ E) is a bare sandspit close to Vlieland and one of the key roosting sites for birds foraging in the western part of the Wadden Sea (van Gils *et al.* 2006). We hypothesized that, due to their decreased manoeuvrability, the heaviest birds should show the highest tendency to skip the roost at Richel after having experienced increased predation danger there. We performed our investigations just before Peregrines would arrive from their northerly (e.g. Scandinavian) breeding grounds to their staging or wintering areas in the Wadden Sea. We planned to induce predation danger by controlled raptor intrusions. Yet, as we could not get hold of a falconer and tethered falcon, we used a remote controlled aeroplane instead. We found a dedicated hobbyist who was not only able to fly with a radiographic aeroplane, but who was also skilful in constructing such machines. Sadly, the falcon-like profile he applied to a plane hampered its flying properties causing it to crash in a test flight.

We then decided that a 'standard' small and manoeuvrable radiographic plane should do the job. Although the birds would not perceive the plane as a raptor they would at least experience it as a source of disturbance. (Note that all this intrusive experimental work was carefully planned and vetted by the conservation authorities in the Wadden Sea!). On 5 August, at high tide, we flew the plane towards the roost. We performed four successive flights. The first flight created massive disturbance, inducing flight in all birds. When landing, the shorebirds, and Curlews *Numenius arquata* in particular, more closely packed together then they had previously done. The second and third flight emitted weaker responses, but still a lot of birds left the roost altogether after the fourth flight. In the course of August we added three of such disturbance experiments, each consisting of three or four short successive flights, while recording which birds were present before the intrusion and which individuals returned in the next roosting session.

As the operator of the plane could not continuously be present, and weather conditions not always allowed for flights, we had to take our chances when he was present. As not all radiotagged birds used Richel as a roosting place at all times, sample sizes were often quite moderate (ranging from 4 to 21 birds present) which limited statistical power. This may have been the reason that in the end we did not

Figure I.1 Observation tower in the Wadden Sea. In 2004 Red Knots were kept in wire-netting cages below the observation platform.

find any effects of body mass on the birds' decisions whether to roost again on Richel after being disturbed.

Therefore, the next year we decided to repeat the experiment. To increase detectability of effects we decided to create weight categories ourselves by catching birds, holding them in a pen on the lower deck of our observation tower (Figure I.1), and feeding them with Brown Shrimp *Crangon crangon*, differentiating in feeding ration such that one group would end up as the heavy ones, the other as the light ones. These two groups would then be released and exposed to predation danger while at the roost. Meanwhile we had succeeded in engaging a falconer with a large (and quite lazy) Saker Falcon *Falco cherrug* (Figure I.2) to perform a real predation disturbance job.

Although straightforward at first sight, creating weight classes by differential feeding turned out to be a tough job. Not only was it difficult to keep the shrimps alive (we kept them in large tubs; we added oxygen and kept densities as low as possible), it was plainly impossible to induce birds to put on weight. Although we went to extremes to feed them, all birds tended to lose weight. In the end, birds were released with body masses that were on average 17 g less than their body masses at catch. As we were not able to create two weight classes of birds, we decided, as an alternative treatment, to clip the 7th or 8th primary (ones that they

Figure I.2 Saker Falcon used in the 2004 experiments. Richel (and the island of Vlieland behind it) is on the background.

were about to shed) in half of the birds in order to temporally induce a small flight handicap nevertheless, seeing whether this would influence their roost decision after being exposed by our Saker Falcon. The falcon was released from the observation tower. Rather than attacking or even targeting shorebirds the falcon just flew to the sandspit and perched on the sand. Although shorebirds flew off at its appearance their responses were not as strong as we would witness after appearance of a wild Peregrine (this fitted the threat-sensitive predator avoidance hypothesis which we would later demonstrate in an experimental context – Chapter 8). Still, hardly any of the birds returned at all to the roost the following days leaving us with virtually no data!

Unfortunately, sensible insights often come with hindsight. For instance, it is likely that by keeping Red Knots in captivity we were actually imposing a predation danger treatment upon them. The fact that the birds kept their body masses low no matter how hard we tried to stuff them with shrimps (a high quality food source, indeed), may, next to other possible stress factors, well have been the reflection of an anti-predation measure (see, for instance, Chapter 9)! Besides, even if we would have managed to create a differentiation in weight classes, we should have been prepared for the possibility that birds adjust pectoral muscle to changes in wing loading in order to maintain flight performance (Chapters 8 and 9).

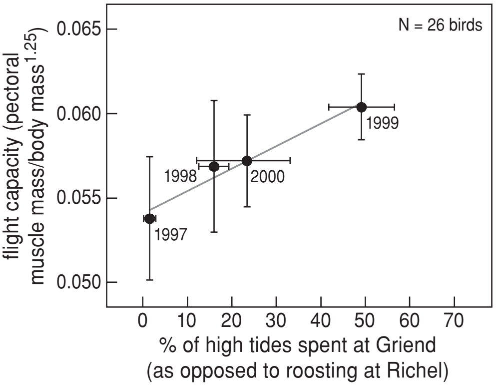


Figure I.3 Flight capacity (pectoral muscle mass/body mass$^{1.25}$ – for further explanation see Chapter 7) as a function of the percentage of high tides spent on the more dangerous roost of Griend compared to the safer roost of Richel.

In fact, a few months later Jan van Gils made a calculation on a small dataset, which suggested that Red Knots trade-off energy costs against safety in choosing roost site. It involved a comparison between birds choosing either Richel or Griend as a roosting site. Richel is a bare sandspit that due, to the absence of landscape structures that could conceal raptor attacks, was considered to be much safer than Griend that is largely bordered by a dyke. As Griend is closer to the principal feeding grounds it was hypothesized that birds would trade-off a roost entailing low energetic and time costs of travel but relatively dangerous (Griend), against a roost with relatively high energetic and time costs of travel but low predation danger (Richel), while this trade-off should depend on the potential for successful escape on attack being determined by the ratio of pectoral muscle to body mass (Dietz *et al.*, 2007). Indeed, Van Gils found that Red Knots that spent more time at the risky roosting site maintained a relatively larger pectoral muscle (Figure I.3), thus appeared to be better suited for escape.

Recapitulating, imperfections in research designs, and limited opportunities for systematic measurements of raptor-shorebirds interactions in the Wadden Sea compared to Banc d'Arguin, explain why the latter area became the core field site for the predation studies in this thesis.

CHAPTER 2

Dense foraging flotillas of Eurasian Coots *Fulica atra* explained by predation by Ganges Soft-shell Turtle *Aspideretus gangeticus*?

Piet J. van den Hout

ABSTRACT

Overwintering Coots *Fulica atra atra* were observed in January 2006, in Keoladeo National Park, India. Here they fed on aquatic plants, which they exploited in strictly-maintained dense flotillas; these flocks behaved like a super-organism. This observation adds to a description of Ali & Ripley (1969), who do not explicitly discuss the cause of raft formation by Coots, but only mention the occurrence of Coot predation by Greater Spotted Eagle *Aquila clanga*. Having observed a Coot being drowned by a Ganges Soft-shell Turtle *Aspideretus gangeticus*, I suggest that predation risk by these turtles should be taken into account as a possible cause for this herding behaviour. When on the water, Coot flocks now and then suddenly scattered; this suggested disturbance by a hidden aquatic predator, all the more because no raptor attacks were witnessed on these occasions. Coots visited the water exclusively for foraging, and, in contrast to their usual behaviour, roosted on islands. This indicates that they considered the water as a dangerous environment, despite the fact that on land the risk of predation by eagles may be greater. My observations suggest that, by foraging in very dense groups, Coots and other waterbirds exploited the rich food resources in Keoladeo whilst minimising the risk of predation.

Published in 2006 as a short note in *Ardea* **94(2)**: 271–274.

The nominate species of the Eurasian Coot *Fulica atra atra* is widely spread over Europe and Asia (del Hoyo *et al.* 1996). In winter, Coots typically forage in vegetated shallow lakes and ponds. They are omnivorous, feeding mainly on the vegetative parts or seeds of aquatic and sometimes terrestrial plants (Ali & Ripley 1969, Cramp & Simmons 1980, del Hoyo *et al.* 1996). In contrast to their behaviour in the breeding season, wintering Coots generally devote little time to aggression and are gregarious when roosting or foraging (Gibbons *et al.* 1993). Taking plant food, flocking Coots probably suffer only moderate interference costs, and may even optimise cropping rates by carefully timed visits, as reported in geese (Prins *et al.* 1980, Prop & Loonen 1989). Nevertheless, the most important reason for Coots to flock may be their vulnerability to predators (Randler 2005), as their agility is limited and they occur in open habitats (Glutz von Blotzheim *et al.* 1973, Cramp *et al.* 1993). Studies on several aquatic predators demonstrated a decreased probability of attack as group size of prey increased (Neil & Cullen 1974, Treherne & Foster 1982).

The nature and level of predation on Coots varies, of course, and this may be reflected in regional differences in habitat use. Wintering Coots in Western Europe, when disturbed, retreat to open water, which is apparently a safer habitat than land. Likewise, flocks tend to roost on open water (Cramp & Simmons 1993, Bijlsma *et al.* 2001), and when feeding, if not on water, they mostly do so near the water's edge, ensuring escape routes towards the water (Glutz von Blotzheim *et al.* 1973, Irwin & O'Halloran 1997). These may all be adaptations to terrestrial predators such as Red Foxes *Vulpes vulpes* and raptors. Although Coots on the water occasionally may be caught by Goshawk *Accipiter gentilis* (van Hattum 2002, van den Brink 2003, Jaschke 1996), the risk of predation is presumably negligible compared to when on land.

One would expect the pattern to be reversed when predation pressure on water is higher than on land, and this is what seems to occur in at least one locality in Northern India. In January 2006, in the Keoladeo Ghana National Park, Bharatpur, India (27°13'N, 77°32'E), a 29 km^2 natural floodplain of the Gambhir and Banganga River (Middleton 1992), I observed Coots foraging in extremely dense flocks (ranging from about 200 to at least 500 individuals) on submersed water plants (probably mainly Floating Haert *Nymphoides cristatum* and Water Snowflake *N. indicum*; B. Middleton, pers. comm.) which they took mainly from just below the water surface (Fig. 2.1A). Intake rates were not quantified, but were substantial. The Coots, which were abundant in Keoladeo, roosted exclusively on the small vegetated islands that were scattered over the floodplain, and avoided the water except for foraging. When switching from resting to feeding, Coot flocks plunged themselves into the water almost simultaneously, immediately followed by flotilla formation or the merging with an existing flotilla. It was as if invisible ropes tied the birds together (Fig. 2.1B). From time to time such a raft abruptly broke up into a massive centrifugal burst of splattering birds (Fig. 2.1C). In similar terms, Ali & Ripley (1969) describe the 'pattering din set up by such a close-packed herd' of Coots. They do, however, not discuss the cause of this behaviour explicitly but only report to have seen these

Figure 2.1 (A) Coot flotillas in Keoladeo National Park, India; (B) Coots simultaneously leave an island roost to resume feeding; (C) a disturbed Coot flock, with birds fleeing in all directions; (D) Coot being drowned by a Soft-shell Turtle.

responses after a gunshot or an attack by an eagle. Elsewhere they note that wintering Coots may suffer greatly from predation by Greater Spotted Eagles *Aquila clanga* (Ali & Ripley 1968). Nevertheless, although Greater Spotted Eagles were around in Keoladeo, and are known to swoop low over Coot rafts to scatter them in order to isolate and capture a prey individual (Ali & Ripley 1968), in neither of the many cases in which I spotted this fleeing behavior of a Coot raft, Coots were under eagle attack. Yet, as I did not have full view of the sky at all times I cannot exclude the possibility that soaring eagles elicited the fleeing response. Nevertheless, the behaviours – flocking and fleeing – could also be explained by the threat of a hidden aquatic predator, a possibility Ali & Ripley did not mention. A good candidate is the Ganges Soft-shell Turtle *Aspideretus gangeticus*. These turtles were regularly spotted resting on mud banks. One late afternoon I spotted a Coot being slowly drowned by what was very likely such a turtle (Fig. 2.1D). Although the Coot managed to resurface several times, again and again it was dragged under, until at last it disappeared for good, parting from life with a few bubbles.

The Ganges Soft-shell Turtle, with a carapace length of up to 70 cm, is known to be largely carnivorous (Daniel 1983), and researchers working in the Keoladeo National Park confirmed predation on adult Coot by Ganges Soft shell Turtle (B. Middleton, pers. comm.). In fact, in Keoladeo two big Ganges Soft-shell Turtles were observed to pull down an apparently injured Nilgai *Boselaphus tragocamelus* (Singh

2000). This is a large, horselike built antelope (shoulder height 120–150 cm, and weight 109–288 kg; Prater 1971), and while it struggled many other turtles gathered, biting off chunks of flesh from the flanks of the animal (Singh 2000). Moreover, Soft-shell Turtles have been recorded taking waterfowl, millipedes, fish and flapshell turtle (*Lyssemys* sp.) alive and scavenging on dead fish and mammals (Singh 2000). I propose that the Soft-shell Turtles cannot be ignored as a possible serious predator when judging the sense of raft formation in Coots. Furthermore, Coots treated the aquatic environment as dangerous, in contrast to relatively safe islands on which they roosted, despite the fact that on land eagles may cause the greatest risk of predation.

When feeding on the water in very dense flocks the Coots may look like very large unprofitable organisms to the turtles. In any case, individual risks of predation would be 'diluted' in such flocks (e.g. Hamilton 1971, Foster & Treherne 1981, Godin 1986). Correspondingly, Eurasian Teal *Anas crecca* were often observed merging in the Coot flotillas in shallow water, whereas Northern Pintails *Anas acuta*, like Coots, formed very dense foraging flocks as well. All these waterbirds only roosted on islands of dry land.

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Chapter 3

Extreme head posture of birds: predation detection or sun avoidance?

Piet J. van den Hout and Graham R. Martin

ABSTRACT

Observers tend to derive the direction of attention of a scan from the head posture of the bird, and a tilted position of the head is commonly interpreted as scanning the sky for predators. However, contrary to humans, many birds have two or more areas in each retina that are specialized for high-acuity vision. This implies that, particularly in monocular vision, head angle may not always reliably tell us were a bird's attention is actually directed or what part of the visual scene the bird is examining in detail. We report insightful observations on extreme head tilting behaviours in two shorebird species, Baird's Sandpiper *Calidris bairdii* and Puna Plover *Charadrius alticola* foraging at midday, and under a clear sky, on a salt plain in Chile. From the viewpoint that careful interpretation of head postures is essential when studying anti-predation vigilance of foragers, we discuss whether such head postures may be a manifestation of a particular type of vigilance behaviour whose primary function is the detection of predators in the sky, or also the avoidance of disability glare produced by imaging the sun on the retina, which generally reduces image quality across the entire visual field.

Submitted for publication

INTRODUCTION

Sensory ecology investigates the information that underlies an animal's interactions with its environment (Dusenbery 1992). Relationships between the sensory challenges posed by particular environments and the information that organisms extract from them have been described in general terms, and some interesting examples of how sensory capacities are linked to particular behaviours, and tuned to particular sensory challenges, have been described in birds e.g. olfactory guided foraging in seabirds (e.g. Nevitt 1999, 2010), visually guided foraging in turbid water in amphibious predatory birds (White *et al.* 2008), and tactile cues in birds which probe in soft substrates (Piersma *et al.* 1998, Cunningham *et al.* 2007, Zweers and Gerritsen 1997). Such examples frequently show that there are trade-offs both between sensory systems and within a sensory modality when trying to optimize the capture of information in order to carry out certain tasks, especially where tasks have to be conducted simultaneously. A prime example of this lies in the topography of visual fields. It has been argued that there is a trade-off between the position of eyes in the skull so as to provide visual control of bill position, and their position that would give comprehensive visual coverage to maximize the detection of predators (e.g. Martin & Piersma 2009). While natural selection might favor in most birds comprehensive or extensive visual coverage above and about the head for predator detection, this often appears to be compromised by the need for the visual control of the bill (Martin 1986, 2009). Only in birds which do not need to use their bill for foraging, provision chicks or nest construction (certain ducks Anatidae and long-billed shorebirds Scolopacidae) is comprehensive visual coverage above and about the head achieved (Martin 2009).

Anti-predation vigilance, also referred to as scanning for predators, is usually defined by behaviours that involve raising the head above the level of the body while holding it approximately vertical, and perhaps also rotating the head about its vertical axis (a yaw movement of the head) (Lima 1990, Caro 2005). However, depending on the visual field of the species (Martin 1994, Fernández-Juricic *et al.* 2004), it has been argued that some level of predator vigilance can be maintained even with the head pitched forward or placed at or close to a foraging surface (e.g. Lima and Bednekoff 1999a, Guillemain *et al.* 2002). This applies especially where there is significant visual coverage above and behind the head as occurs in some shorebirds Scolopacidae and wildfowl Anatidae. However, birds sometimes adopt other more extreme positions of the head, especially extreme rotations about the roll axis, as illustrated in Fig. 3.1. We ask whether such extreme head tilting is a manifestation of a particular type of vigilance behaviour.

Observers tend to derive the direction of attention of a scan from the head posture of the bird (Metcalfe 1984, Lima & Bednekoff 1999a), and a tilted position of the head is commonly interpreted as scanning the sky for predators. However, contrary to humans, many birds have two or more areas in each retina that are specialized for high-acuity vision (Dawkins 2002). This implies that, particularly in

Figure 3.1 (Photographic examples of extreme head tilt postures recorded in a Puna Plover (A) and Bairds Sandpiper (B). These were recorded at a location close to the equator when the observer approached the birds at about midday when the sun was high overhead in a clear sky (see casted shadow).

monocular vision, head angle may not always reliably tell us were a bird's attention is actually directed or what part of the visual scene the bird is examining in detail (Dawkins 2002).

The problem of detecting dangers in the sky

Although extensive or comprehensive vision may serve to give birds early warning of a predator's approach, a further complication arises from two factors:

(1) Comprehensive or extensive visual coverage of the hemisphere about the head means that if the sun is in the sky it must be imaged somewhere upon the retina. This can clearly have detrimental effects not only on the portion of retina on which the sun is imaged but also on the quality of the image across the rest of the retina (Martin & Katzir 2000, Martin & Coetzee 2004).

(2) The highest optical quality, and therefore probably highest acuity within the visual field of each eye, occurs along its optical axis (Lythgoe 1979, Archer *et al.* 1999, Cronin 2008). However, in order to achieve comprehensive vision the eyes must be placed laterally in the skull and so the regions of highest acuity project laterally from either side of the head, not frontally. The use of lateral vision in the control of tasks requiring high resolution seems well established (Martin 2009). Even the task of stooping upon prey a Peregrine Falcon *Falco peregrinus* seems to use lateral rather than frontal/binocular vision, since it has been shown that the bird approaches along a curving path which allows the prey object to be kept in the vision of the laterally projecting fovea of one eye until the final closure upon the prey object when transfer is passed to frontal vision as close range (Tucker 2000, Tucker *et al.*, 2000). This use of lateral vision to detect an object and the control of behaviour passing to the frontal field only when the object is in close proximity, is

similar to that described in thrushes Turdidae (Montgomerie & Weatherhead 1997), Zebra Finches *Taeniopygia guttata* (Bischof 1988, George *et al.* 2006), Rock Pigeons *Columba livia* (Bloch *et al.* 1988) and domestic chicks *Gallus domesticus* (Dharmaretnam & Andrew 1994).

METHODS

Anecdotal observations are sometimes reported which indicate that a bird appears to use lateral vision to look upwards (tilting the head through a large angle) in order to detect aerial predators and anticipate the appropriate escape response (Walls 1942, Fernàndez-Juricic *et al.* 2004). To this we add an 'insightful' observation on head postures of two shorebird species (Baird's Sandpiper *Calidris bairdii* and Puna Plover *Charadrius alticola*) that were foraging and resting on a salt plain in the Atacama Desert, Chile, on 24 January 2005, in the middle of the day.

RESULTS

When approached at close range – up to approximately 5 m (Baird's Sandpiper) and 10 m (Puna Plover) – by the observer, individuals of both Baird's Sandpiper and Puna Plover frequently tilted their head (rolled it about the sagittal axis) as if scanning the sky (Fig. 3.1). The sun was at high elevation in the sky. At the time of the observations not a single raptor in the sky could be found by the observer. Both shorebirds were alone, that is, not accompanied by conspecifics.

DISCUSSION

Why did these birds display these head postures? As no raptors could be detected it was likely that the behaviour was not a coincidence between the birds happening to detect a raptor in the sky just when the observer was approaching. It seemed that it was the approach of the observer that triggered this head tilting behaviour. Our interpretation is that the birds perceived the approaching observer as a threat (i.e. a ground based predator) and were preparing to make an aerial escape response (checking the sky in anticipation of take-off) should the ground based predator get too close. However, escaping would possibly make the birds more vulnerable to any aerial predators in the vicinity.

Perceptually, however, two factors may be coming into play. First, it seems highly likely that the birds are tilting their heads so as to bring high acuity lateral vision to examine the sky. Secondly, the birds could be trying to reduce the adverse affects of imaging the sun upon the retina and this may be so as to gain better quality information about the ground based predator that is approaching or maximizing the chances of detecting a possible aerial predator above them. Imaging the sun can not only cause temporary blindness within certain parts of the visual field as a result of extensive bleaching of the photopigments in the photoreceptors, but the sun's image can itself act a secondary source of light within the eye, scattering light generally across the retina reducing acuity across much of the visual field (Martin 2007).

Reducing such scattered light could in fact be overcome by positioning the eye so that the image of the sun falls directly upon the pecten. The pecten is a highly pigmented black structure that extends from the retinal surface into the posterior chamber of the eye (Martin & Piersma 2009). Its prime function is to provide nutrition for the retina; avian retinas lack the network of blood vessels which characterize the mammalian retina. The pecten is situated above the point where the optic nerve exits and extends perpendicularly from the retinal surface (Martin 1985). It produces a relatively large blind area within the visual field of each eye. As well as its nutritional function the pecten may additionally serve other functions and many hypotheses have been proposed (Mann 1924, Brach 1977). The dark pigmentation and somewhat velvety texture of the pecten surface indicates that the pecten absorbs light strongly and it has been suggested that the pecten reduces glare caused by bright sunshine hitting the cornea (Brach 1977), i.e. it intersects and absorbs stray light within the eye. However, Brach (1977) did not seem to include the possibility that birds, by adjusting head posture, may actually ensure that the image of the sun falls directly onto the pecten in order to reduce the likelihood that light is scattered within the eye (Fig. 3.2).

We propose that the head tilting behaviour in birds of the kind described here is linked to aerial predator detection or to gaining a better image of the approaching ground predator (the approaching observer), and it could be serving these two functions simultaneously. First, tilting the head to allow one eye to look skywards brings more central parts of the lateral visual field, in which acuity is likely to be highest, to examine the sky and thus increase the chances of correctly identifying a predator threat. Second, it may also serve to reduce the generally detrimental effects on images throughout the visual field of imaging the sun when looking into the sky. This would be achieved by ensuring that the sun's image falls upon the non-visually sensitive pecten and reduces the probability that light is generally scattered within the retinal image. The angular maximum width of each pecten in a shorebird is about 20° and its vertical extent is about 40° (Martin & Piersma 2009). The angular width of the sun is only 32 arc minutes, thus the visual angle occupied by each pecten is >1500 times larger than the image of the sun (See Appendix 1). Therefore placing the image of the sun in the blind area generated by a pecten does not require high accuracy and would allow a bird to move its head while still ensuring that the sun's image fell within the blind area.

Clearly differentiating between these functions of directly scanning the sky for predators or avoiding imaging the sun is problematic and indeed they may both function simultaneously. However, further systematic field observations could perhaps help to distinguish between the prime and secondary functions of this head

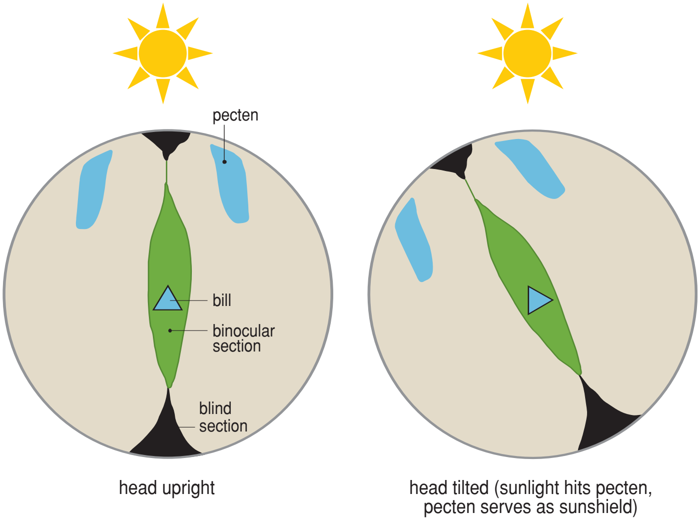

Figure 3.2 Illustration of general mechanism that underlies our suggestion that by adjusting head posture, a bird could ensure that the image of the sun falls directly within the blind area formed by the pecten. The circles represents a simply three dimensional projection of the frontal half of the visual field of a shorebird that is looking forwards directly out of the page. There is a long and narrow area of binocular overlap in the fontal field that looks directly ahead and the blind areas produced by the pectens project upwards and slightly laterally in the fields of each eye (Martin & Piersma 2009). The sun is directly overhead. In the left hand diagram the head is upright. In this situation the image of the sun will fall on both retinas. The right hand diagram illustrates that by tilting the head (rolling the head about its long axis and therefore rotating the binocular field and the projections of the blind areas formed by the pectens) the image of the overhead sun can be made to fall on the pecten. In this the image of the sun will fall on the pecten of the left eye while the right eye will not be able to image the sun at all as it will be facing towards the ground. As noted in the text there is a large difference in the angular size of the blind area produced by a pecten and the size of the image of the sun (but we have not been able to capture that difference in this diagram). Because of this size difference a bird would not have to position its head with high accuracy to ensure that the sun is not imaged upon the retina. Clearly if the sun is not directly overhead the head can be tilted to different angles to ensure that the sun's image still falls on the pecten of the eye that faces the sky.

tilting behaviour. Observations of head tilting should also take into account that there is increasing evidence that birds use different eyes and hence different halves of the brain for different tasks (reviewed in Rogers 2008). This evidence is derived from a number of studies which indicate that the left hemisphere/right eye is used preferentially for tasks involving the separation of pertinent stimuli from distracting stimuli (e.g. food from pebbles, odor cues from attractive visual cues, magnetic cues from other cues indicating location), whereas the right hemisphere/left eye is used for tasks requiring broad attention and is easily distracted by novel stimuli. Rogers (2008) proposed that the right hemisphere/left eye also controls fear and escape responses, as in reaction to predators. However, fear perceptions are hard to interpret and birds may alternate the use of left and right eye in confrontations with predators, probably in correspondence with the level of danger. For instance, Australian Magpies *Gymnorhina tibicen* that were confronted with a Monitor Lizard *Varanus varius* appeared to use the right eye/left hemisphere to process visual inputs prior to approaching this predator and the left eye/right hemisphere prior to withdrawing from it (Koboroff *et al.* 2008). Our observations, at least in those of the Baird's Sandpiper, showed that the head was tilted to look at the sky with both the left and right eyes; note that the Puna Plover is scanning with its right eye (Fig. 3.1A). However, the sample size of our observations is small and we are simply recording here that this behaviour does occur regularly under certain conditions. We would hope that other observers will also be able to gather data on this behaviour in a wide range of bird species.

We suggest that when such obvious "looking" behaviour as show in Fig. 3.1 occurs it would be very valuable to gain systematic data on not only the spatial relationship between the bird and the threatening ground predator (the observer) but also on the presence and position of the sun relative to the head angle of the bird. The observations reported here occurred under conditions when the sun was at high elevation in a clear sky. Does this behaviour occur when the sun is lower in the sky or absent? Such observations may make it possible to determine whether the birds are head tilting in order primarily to reduce the detrimental effects of imaging the sun to ensure that it falls upon the pecten, or whether they are simply bringing the region of highest acuity to look skywards.

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APPENDIX 1

In order to measures the relative size of the blind area created by the pecten to the size of the sun's image, we expressed sizes of pecten and sun in steradians, Ω, the SI unit for solid angle. The solid angle (in number of steradians, Ω) of the simple cone subtending an angle Θ is given by:

$$\Omega = 2 \pi (1 - \cos \Theta),$$

As Θ is half the angle α, at the base of a solid cone, the expression can also be written as

$$\Omega = 2 \pi (1 - \cos (\alpha/2)),$$

where α is the solid angle at the base of the cone.

We then calculate how many times a cone the size of the sun as seen from earth (α = 32 arcminutes = approximately 0.5^o) would go into a cone which has an angular size similar to that of the pecten (we have assumed that the pecten projects as a circular cone of 20^o , however, this would be an underestimate since the pecten is in fact larger than this). We get:

$$2 \pi (1 - \cos (20°/2)/ 2 \pi (1 - \cos (0.5°/2) = 1596 \text{ times.}$$

Box II

Mortality-driven versus fear-driven predator-prey dynamics

Predator-prey interactions involve two opposing selection pressures as the predator's ability to catch and kill prey is counteracted by the prey's ability to avoid predation. Yet, this interaction is asymmetric, as an individual prey has more to lose by failure to avoid a predator, than predators by failing to catch a prey. To be able to work with the prey's and predator's asymmetric and opposing selection pressures, Brown *et al.* (1999) introduced the concepts of 'fear-driven population interactions' as opposed to 'mortality-driven interactions'. This distinction was inspired by the "r/a" measure of apparent competition by Holt (1977). The N-driven component reflects the prey's intrinsic growth rate r in the face of predation. The fear-driven component measures the predator's ability to catch prey, in other words the predator's rate of encountering the prey, a.

Brown *et al.* (1999) define 'fear' as an organism's perceived cost of injury or mortality. In contrast to mortality-driven systems, in a fear-driven system the predators do not appear to control their prey's population through mortality. Contrary to fear-driven systems, in mortality-driven systems predators would *"have little effect on the behaviour of their prey"* (italics PJH) and would influence the dynamics and abundance of prey only through direct mortality (Brown & Kotler, 2007). Classic predator-prey models like the lynx-hare cycle and the weasel-vole-cycle are suggested to be typical mortality-driven systems.

Although it is perfectly understandable that anti-predation behaviour limits predation rate in fear-driven systems, how *the lack of* anti-predation measures would be the *ultimate* cause of mortality-driven dynamics remains largely implicit. This is unfortunate, especially because the statement is not readily intuitive. Firstly, because natural selection would be expected to penalize relaxed anti-predation traits; secondly, because the argument that fear-driven systems are dominated by the intimidating influence of fierce predators (Brown & Kotler, 2007) implicitly suggests that the predators (like Canada Lynx *Lynx canadensis*) in mortality-driven systems (like the lynx-hare cycle) would not be fierce enough to scare their prey. In fact, fear-driven (non-lethal) effects were ubiquitous in Snowshoe Hares *Lepus* *americanus* (Hik, 1995, Sheriff *et al.*, 2009), in Arctic Ground Squirrels *Spermophilus parryii* (Karels *et al.*, 2000) and House Mice *Mus musculus* (Arthur *et al.*, 2004). Thirdly, because it does not explain why, for instance, Snowshoe Hares (actors in a supposedly N-driven system) would be less “sophisticated” in escaping from lynx than squirrels from foxes (actors in a supposedly fear-driven system).

Essentially, high levels of direct consumption by predators occur as a result of density effects among rapidly increasing prey populations, which prey overcome with large reproduction potential. Such density-dependent effects may include the lack of refuges inevitably exposing more prey to predators, which then can feast on this booming population until decreasing numbers of prey forces them to shift to alternative prey (Newton, 1998). Rather than being an attribute of the predator, it is the prey, through density-dependent effects causing its anti-predation measures to be less effective, that causes high mortality. So, even if this behaviour would be regarded as ‘fearless’ behaviour, it seems at best the proximate cause of mortality, but not the ultimate one; density-dependence is.

PART II

LETHAL AND NON-LETHAL EFFECTS OF PREDATION AND PREDATORS ON SHOREBIRDS

CHAPTER 4

Differential mortality of wintering shorebirds on the Banc d'Arguin, Mauritania, due to predation by large falcons

Piet J. van den Hout, Bernard Spaans and Theunis Piersma

ABSTRACT

Predators may influence many aspects of the daily life and seasonal movements of their prey. Here we quantify direct, and evaluate indirect effects of predation by three falcon species (Lanner Falcon *Falco biarmicus*, Barbary Falcon *Falco pelegrinoides* and Peregrine Falcon *Falco peregrines*) on coastal shorebirds wintering on the Banc d'Arguin, Mauritania, an area hosting approximately 30% of the East Atlantic Flyway population of shorebirds. On the basis of 754 h of observation over five winters, 97 witnessed attacks and 585 collected prey remains, we show that shorebirds were safer in larger flocks, which tended to be attacked less often. Furthermore, species that forage relatively close to shore and in small flocks were depredated more often than expected from their relative abundance. In three species, Red Knot *Calidris canutus canutus*, Bar-tailed Godwit *Limosa lapponica taymyrensis* and Dunlin *Calidris alpina*, the juveniles were more vulnerable than adults. We estimated that on average 1% of the juvenile and 0.1% of the adult Red Knots present were killed by large falcons each winter. For Red Knots we simultaneously quantified annual survival on the basis of an individual colour-marking programme: mortality due to predation by falcons accounted for an estimated 6.2% (juveniles) and 0.8% (adults) of annual mortality. We suggest that juvenile Red Knots are 10 times as likely to be killed by falcons because they use riskier habitats, i.e. early and late tide foraging areas closer to shores where surprise attacks are both more common and more successful. These results indicate that the strength of indirect effects of predation operating in a shorebird population largely outweigh the effects of mortality *per se*.

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INTRODUCTION

Coastal shorebirds have much to fear from fast aerial predators, especially falcons (Dekker 1980, 1988, 2003, Bijlsma 1990, Buchanan 1996, Fuller *et al.* 1998, McGrady *et al.* 2002, Ydenberg *et al.* 2004). Even if predators kill few animals relative to the total population, these predators may have non-lethal, indirect effects on bird numbers and distributions via behavioural decisions of the prey, which could far outweigh the lethal effects (Newton 1998, Lind & Cresswell 2005). For instance, differences in death rates between classes of individuals (i.e. species or age-classes) could result from differences in the ways that they trade-off starvation and predation (e.g. Lima & Dill 1990). Therefore, mortality per se is not the relevant measure of total predation impact (Lank & Ydenberg 2003, Lind & Cresswell 2005, Ydenberg *et al.* 2007). Such indirect effects have been claimed in a number of studies on various invertebrate and vertebrate animal species (Sih *et al.* 1985, Anholt & Werner 1995, Nakaoka 2000, Creel *et al.* 2007, Heithaus *et al.* 2007).

For several coastal sites it has been documented that avian predators kill a sizeable part (up to half) of the available shorebirds over single winter periods (Page & Whitacre 1975, Whitfield 1985, Cresswell & Whitfield 1994). However, it is quite possible that atypical sites with high raptor attack rates have attracted students of raptor predation. To put predation by raptors in proper demographic and evolutionary contexts (e.g. see Lima & Dill 1990, Lank *et al.* 2003, Ydenberg *et al.* 2004), we need estimates of mortality rates from major wintering sites, i.e. sites selected on the basis of their importance for shorebirds, rather than for the ease of witnessing raptor predation.

With two million wintering shorebirds, about one-third of the entire East Atlantic Flyway population (Altenburg *et al.* 1982, Smit & Piersma 1989, Zwarts *et al.* 1998a, Davidson & Stroud 2006), the Banc d'Arguin in Mauritania clearly qualifies as a site of major importance. Building on a major research effort to quantify annual survival and site faithfulness in Red Knots *Calidris canutus canutus* (e.g. Leyrer *et al.* 2006), we have embarked on a study of the impact of predation by raptors relative to overall rates of mortality. We here present the full dataset accumulated over five consecutive winters on rates of attack, attack success and prey selection by aerial predators.

STUDY AREA AND METHODS

Study area

The Banc d'Arguin is an area of shallow water and islands that stretches along the northern coast of Mauritania, bordering the Sahara desert from about 20°50'N, 16°45'W to 19°20'N,16°28'W. Part of this area, including 500 km^2 of intertidal flats, is protected as a national park. The Parc National du Banc d'Arguin covers a total of 12 000 km^2, 6300 km^2 of which is open shallow seas (Altenburg *et al.* 1982, Wolff & Smit 1990, Isenmann 2006).

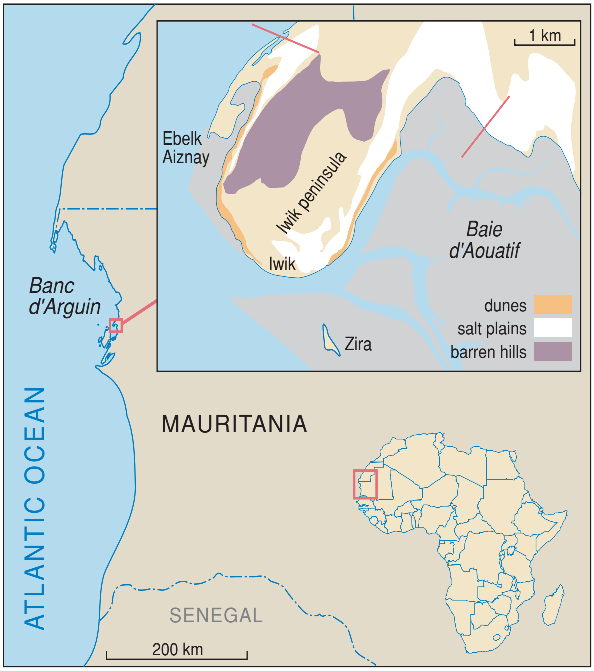

Figure 4.1 Map of the study area. Records of raptor attacks are confined to the coastal zone of the Iwik peninsula between the red strokes north of Ebelk Aiznay and in the Baie d'Aouatif. The central purple area are the barren hills were large falcons usually rest and from where they launch the majority of their attacks. The sebkha (salt plains) are depicted in white, whereas the dunes that border the mudflat are shown in orange.

The fieldwork was carried out on and around the Iwik peninsula (19°53'N, 16°17'W, Fig. 4.1), named after the fishing village of Iwik (around 200 inhabitants), an area which we assume to be representative for the entire Banc d'Arguin. Of a total area of 50 km^2, approximately 22 km^2 is occupied by tidal mudflats, which are largely covered by seagrass (*Zostera* spp.), salt plains (sebkha) and desert. Two shallow bays are located on either side of the peninsula. Northwest of Iwik is Ebelk Aiznay and northeast of the village lies a much larger bay, the Baie d'Aouatif (Fig. 4.1). At Ebelk Aiznay and along the eastern part of the peninsula the mudflats are separated from the sebkha by low dunes covered with a sparse vegetation of succulents (Fig. 4.2). The central part of the peninsula consists of low barren hills (not higher than around 15 m).

Raptor observations

This study was carried out from 2002 to 2006, with five consecutive winter visits of several weeks. A total of 754 h were spent on raptor observations, of which approximately 75% were 'systematic' observations, i.e. observations that were not combined with other activities such as shorebird foraging studies or searching for colour-marked birds.

Large falcons were identified to species, and sex and age if possible. Three species, Lanner Falcon *Falco biarmicus*, Barbary Falcon *Falco pelegrinoides* and Peregerine Falcon *Falco peregrines*, were encountered. Records were kept of their hunting efforts with respect to location and tidal cycle (see Dekker & Ydenberg

Figure 4.2 The landscape on the Iwik peninsula: the barren hills on the left provide resting places for the falcons. The dunes bordering the mudflats are used by the falcons to launch stealth attacks (photo by F. Robin).

2004). Furthermore, hunting method, flock size attacked and the result of the attack (success or failure) were recorded. Hunting methods included low level surprise attacks, open attacks, stoops from soaring position and co-operative hunting (Dekker 1980, Bijlsma 1990). In line with most studies, an attack was considered as an attempt to seize or knock down an individual prey during a hunting flight (Kus *et al.* 1984, Buchanan *et al.* 1988). When a raptor changed target, for example after a shorebird flock had broken up into smaller units, we recorded this as multiple capture attempts (Page & Whitacre 1975). When a bird was captured, this was considered a successful attack.

The hills of the central part of the peninsula (Figs 4.1 & 4.2) were favourite perches for the falcons and were points of departure for attack flights. All but one of 97 observed hunting flights (in 575 h of observation time) took place on the peninsula. Attack rate and mortality due to predation were calculated with respect to the coastal area around the Iwik peninsula only (Fig. 4.1). This should cover most if not all predation events in the general study area as no falcon hunts were recorded on the outer mudflats during 22 h of observation (see Fig. 4.1). The area east of the black line in Figure 4.1 was not included because only 27 h of observations were spent there.

Prey remains

During all field periods we systematically searched the coastline for prey remains, which were collected and identified to species. Red Knot, Dunlin *Calidris alpina* and Bar-tailed Godwit *Limosa lapponica taymyrensis* were identified as adults or juveniles following Prater *et al.* (1977). Jackals *Canis aureus* scavenged for dead and dying prey and their prey handling could be easily distinguished from that of large falcons, as Jackals bite off feathers, whereas falcons pull out feathers one by one and leave the wings, sternum and girdle largely intact (Bijlsma 1990).

Bird counts

Once in each of the winter periods, simultaneous high-tide shorebird censuses, by 8–10 people, were executed (Table 4.1). In 2002–03 no counts were available for the island of Zira (see Fig. 4.1), and thus for estimates of direct mortalities we used counts from 2004–06 only.

During 13–23 December 2006 at Ebelk Aiznay, bird numbers were counted over four tidal cycles in a quadrant of 100×75 m on eelgrass (N. Spaans pers. obs.), which gave us a picture of forager abundance until habitat became unavailable due to high tide. Throughout the studies, we made notes on differences in shorebird habitat use, such as distance from cover. This was done separately by species and, for Red Knot in particular, by age-class. Detailed mechanisms concerning age-related habitat use in Red Knots will be reported elsewhere (P.J. van den Hout unpubl. data - Chapters 5 and 6). Following methods in Piersma *et al.* (1993) for Red Knot at Ebelk Aiznay, in December 2006 P. de Goeij recorded the frequency distribution of the size of Red Knot flocks encountered.

Mist-net trapping and survival analyses

Each winter we trapped shorebirds with mist-nets during the calm nights around the new moon with the highest water levels (B. Spaans unpubl. data). This enabled us to determine body masses (which we used for raptor requirement calculations) and age-proportions (particularly for Red Knot, Dunlin and Bar-tailed Godwit) and to mark Red Knots as part of demographic studies. A detailed study in Scotland showed no evidence that colour-ringing affected predation mortality (Cresswell *et al.* 2007).

Table 4.1 Study period, high tide counts, observation effort and large falcon species present in the study area.

Year	Period	High Tide Counts	Obs. hours	Lanner		Barbary		Peregrine	
				female	male	female	male	female	male
2002	24 Nov-11 Dec	6 Dec	143	1	1	1	1		
2003	11-29 Dec	26 Dec	119			1	1		
2004	28 Nov-17 Dec	17 Dec	66	1	1	1	1		
2005	16 Nov-8 Dec	8 Dec	196	1	1	1		1	1
2006	7-27 Dec	16 Dec	230	1	1	2			

The Red Knots that we caught with mist nets were individually colour-marked. On the basis of resightings of these marked individuals (Leyrer *et al.* 2006) using the standard Cormack–Jolly–Seber method in the software program MARK (White & Burnham 1999), we calculated annual (from summer to summer) survival rate. Removing the effects of transients in the estimate of the first year after capture (Sandercock 2003) for adults, the estimated survival 2 years and more after the year of capture was considered to be the best estimate. The transient-effect is reflected by the low value of Φ_2 shown in Table 4.3; it was considered to be absent for juveniles which remain on the Banc d'Arguin in their first 2 years of life (Piersma *et al.* 1992). Estimates were based on the resighting of 992 individually marked Red Knots. Of these, 244 (193 adult, 51 juvenile) were ringed in 2002, 196 (133 ad., 63 juv.) in 2003, 201 (133 ad., 68 juv.) in 2004 and 161 (139 ad., 22 juv.) in 2005. Because all Red Knots in this sample were ringed on the Banc d'Arguin in November–December, mortality either by starvation, disease or predation of juvenile birds on their first journey from the breeding to the wintering grounds is not included in this analysis.

Calculation of predation rates

Predation rates (kills/h) were calculated by multiplying falcon success (no. kills/no. attacks) from attacks with known outcome by the total number of attacks observed per hour of observation. Because it was often impossible to identify the shorebird species that were attacked, to calculate predation rates for each species we multiplied the overall predation rate by the collective abundance of each species identified in the prey remains that we collected. To estimate the relative mortality ('vulnerability index') of each shorebird species, we subtracted the proportion ($\log_{10}$-transformed) of each shorebird species based on the data collected from species counts at high tide ('expected') from the proportion ($\log_{10}$-transformed) of each species found in the prey remains ('observed'; see Møller & Nielsen 2007). A value of 0.5 indicates that a species was five times more likely to be killed by a falcon than expected based on its relative abundance. We use the term 'vulnerability' as a synonym of this likelihood (predation risk). Vulnerability is affected by a number of factors such as habitat selection, feeding behaviour and flock size (Lank & Ydenberg 2003).

In similar manner, but for each species separately, by comparing the fraction of juveniles as found in the prey remains to the fraction of that age-class among birds caught with mist-nets, we calculated relative mortalities for juveniles in Dunlin, Red Knot and Bar-tailed Godwit. We assumed that our mist-net catching gave an unbiased estimate of age composition although we realize that this is not always and not necessarily the case, especially during small catches at marginal locations and times (Pienkowski & Dick 1976, Clark *et al.* 2004, McCaffery *et al.* 2006). Currently, we have no way to assess the magnitude of any such bias. For species and age-classes, χ^2 tests for goodness of fit were applied to test whether observed prey significantly differed from expectation. When only two groups were compared, as in age-class comparisons, a Yates' correction for continuity was applied (Zar 1999).

For each shorebird species we determined the percentage of annual mortality that could be accounted for by predation. We tallied the number of individuals killed by predators per species throughout the study period (2002–06) and calculated the average number of individuals killed per 7-month overwintering period (Page & Whitacre 1975). These averages were divided by the local number of each species as determined by the high tide shorebird censuses (Table 4.1).

We examined the robustness of the overwintering mortality estimates by comparing total bird mass (including waste) depredated with the estimated requirements of falcons (Whitfield 1985, Whitfield *et al.* 1988). Total bird mass taken by raptors was estimated by expressing the species killed by raptors in body mass equivalents (body mass was derived from mist-net catches). Food requirements of falcons were based on estimates for adult Peregrine Falcons and linearly adjusted to other falcon species according to the raptors' body mass (Cramp & Simmons 1980, Ratcliffe 1993). For temperate climatic conditions we calculated that the food (including waste) needed per day varied from 11.5% of body mass in summer to 15% in autumn for a male Peregrine, whereas for the larger female this amount varied from 13 to 15% of body mass (Ratcliffe 1993). As food requirements are expected to be lower in the semi-tropical conditions of the Banc d'Arguin (Wiersma & Piersma 1994), and taking into account that the female requirement per unit body mass is somewhat smaller than the requirements of the male due to her overall large body size (Ratcliffe 1993), we adjusted requirements assuming a daily food intake at the lower end of the range, i.e. 12% of body mass for males and 13% for females.

RESULTS

Most of the predators present were falcons (Lanner, Barbary and Peregrine), with at least four to five individuals in most years (Table 4.1). A few other avian predators were present (Kestrels *Falco tinnunculus*, Marsh *Circus aeruginosus* and Montagu Harriers *C. pygargus*, and Short-eared Owls *Asio flammea*), which occasionally disturbed but rarely attacked shorebirds during our observations.

We observed an average of 8.9 attacks per day with an attack success of 28% (17 successes resulting from 61 attacks). Based on a normal distribution in Red Knot flock sizes (see Fig. 4.5) we distinguished five flock size categories, and found that small (1–10) to moderate-sized (11–50) flocks tended to be attacked more often (Fig. 4.3). Although no differences were detected in attack successes among flock sizes attacked (Fig. 4.3), in a smaller flock the individual risk to be killed in an attack was obviously higher. The majority of attacks (40 out of 77) were by surprise, 28 attacks were carried out openly and on eight occasions falcons stooped from great height. Co-operative hunting was observed only once by Barbary Falcons. Prey remains contained 91% shorebirds, 7.5% terns and gulls, and 1.6% passerines.

Raptor hunting increased towards high tide, when large numbers of shorebirds were forced to use the nearshore mudflats of Ebelk Aiznay and Baie d'Aouatif

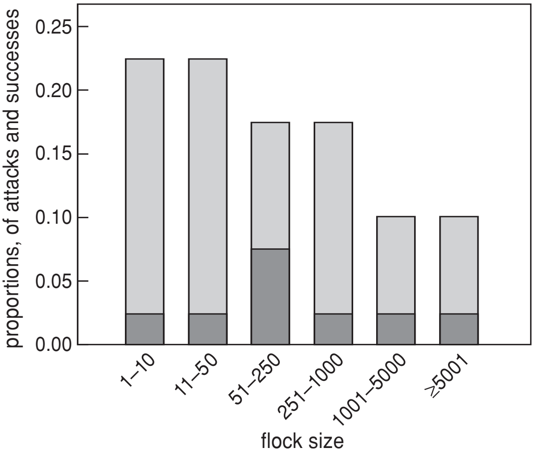

Figure 4.3 Flock size categories as targeted by falcons based on attacks for which the size of the targeted flock was recorded ($n = 40$). Smaller flocks are attacked more often than larger ones. Attack success, which is represented by the black areas of the bars, and only includes the attacks for which the flock size targeted was recorded, shows no correspondence with group size.

(Fig. 4.4A). Nevertheless, as nearshore foraging occurred in large flocks, in this time window the number of attacks per bird hour was fewer, and this was particularly evident for the Red Knot (Fig. 4.4B). In fact, throughout the tidal cycle, the vast majority of Red Knots chose to forage with many flock mates (Table 4.5).

Whimbrel *Numenius phaeopus*, Ruddy Turnstone *Arenaria interpres*, Grey Plover *Pluvialis squatarola* and Ringed Plover *Charadrius hiaticula* experienced the highest mortality (approximately 2% or more of the local population were killed in the wintering area; in Whimbrel nearly 7% were killed), followed by Bar-tailed Godwit, Redshank *Tringa totanus* and Red Knot (slightly over 1%). The estimated direct mortality of Oystercatcher *Haematopus ostralegus*, Curlew Sandpiper *Calidris ferruginea*, Sanderling *Calidris alba* and Dunlin was minor (less than 1% of the local population, Table 4.2).

Dunlin (20 000), Red Knot (12 000) and Bar-tailed Godwit (7500) were by far the most abundant species (Table 4.2). Nevertheless, shorebird species were not killed according to their numerical abundance ($\chi^2_{12} = 470$, $P < 0.001$). Prey vulnerability indices show that Bar-tailed Godwit, Ringed Plover, Ruddy Turnstone, Grey Plover, Redshank, Whimbrel and Red Knot were depredated more than expected from their abundance (Table 4.2). These species also commonly fed alone or in small flocks close to the dunebordered shoreline (Table 4.6), including at high tide when most other birds were roosting. In Red Knot, such birds were mostly (92%) juveniles, as adult birds avoided nearshore mudflats unless the tide made outer mudflats unavailable (P.J. van den Hout unpubl. data - Chapters 5 and 6). Vulnerability cannot be explained by body mass, but seems related to habitat selection (Table 4.6). This is most apparent in two similarly sized species: Whimbrel and Oystercatcher. The former, feeding solitary and close to the shoreline, was seven times more vulnerable than the more gregarious and shore-avoiding Oystercatcher.

For Dunlin, Red Knot and Bar-tailed Godwit the collected prey remains were sufficient to compare relative mortality by predation between juveniles and adults.

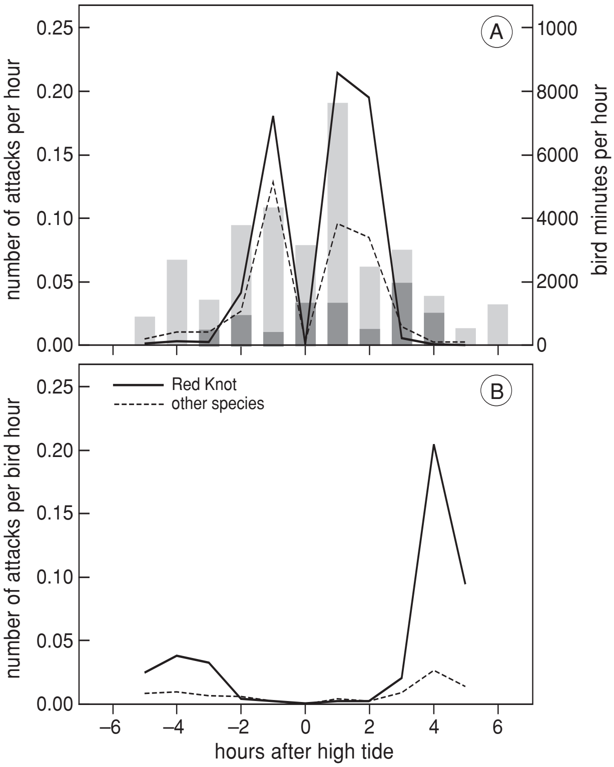

Figure 4.4 A. Hunting pattern over the tidal cycle (shown by bars, dark parts represent successes) with reference to abundance of foraging birds, based on bird minutes per hour as observed in a quadrant in December 2006: Red Knot is represented by the solid line, other species (dotted line) are lumped for ease of viewing. B. Hunting pattern over the tidal cycle expressed as the number of attacks per birds hour: Red Knot is represented by the solid line, other species (dotted line) are lumped for ease of viewing. All data are controlled for observation effort.

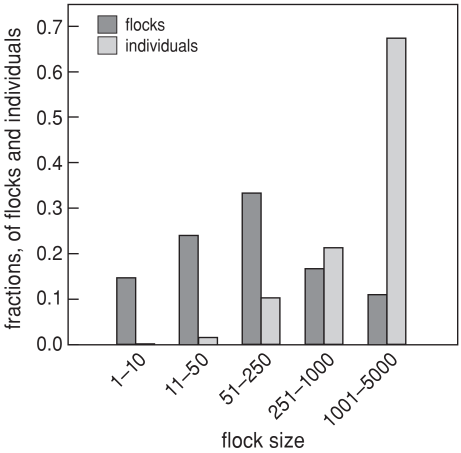

Figure 4.5 Frequency distribution of the size of Red Knot flocks encountered at Ebelk Aiznay in December 2006. Both the fractions of flocks (n = 380) and the fractions of individuals (n = 172,872) experiencing each flock size category are shown.

Based on their relative abundance, Dunlin juveniles were killed 3.5 times more frequently than adults ($n_{\text{remains}} = 66$, $n_{\text{catch}} = 1616$, $\chi^2_1 = 35.5$, $P < 0.001$). In Red Knots this ratio was 5.4 ($n_{\text{remains}} = 103$, $n_{\text{catch}} = 991$, $\chi^2_1 = 199.7$, $P < 0.001$) and in Bar-tailed Godwit the ratio was 2.3 ($n_{\text{remains}} = 62$, $n_{\text{catch}} = 173$, $\chi^2_1 = 36.4$, $P < 0.001$; Table 4.7).

Annual survival in Red Knots was 88.9% for adults and 83.5% for juveniles (Table 4.3). Of the Red Knot population in our study area, 1.1% were estimated to be killed by large falcons (Table 4.2); 92% of these kills were juveniles. Thus, of the annual mortality of 11.1% for adult and 16.5% for juvenile Red Knots, 0.8 and 6.2%, respectively, can be explained by direct mortality due to predation in the wintering area.

Table 4.2 Predation pressure during winter by large falcons on shorebirds at the Iwik peninsula, Banc d'Arguin, Mauritania. The second column (N) shows absolute numbers per species of raptor prey remains found in 2002-06. The third column expresses these numbers as percentages of total remains. Average high tide counts over 2004-06 (± 1SE) are shown in the fourth column. The numbers taken by raptors per month (sixth column) was calculated by multiplying the estimated average number of hunts per day (8.9) by success rate (0.28), and the percentage of that species in the raptor remains. To get an impression of predation mortality during the wintering period (which is around seven months for most species) as a percentage of the population of a species, we assumed a constant predation pressure over all these months (last column). The shorebird species in this table are sorted by decreasing body mass. Terns and gulls, and passerines were lumped for ease of survey. Due to unreliable high tide counts for Little Stint *Calidris minuta*, some calculations were not performed for this species. Prey vulnerability indices are shown in the fifth column (see text and Table 4.6).

Species	N	% in remains	High tide count Avg (SE)	Prey vulnerability index	# taken per month	% of pop. taken in 7 months
Curlew	1	0.2	139 (41)	-0.07	0.1	0.7
Whimbrel	18	3.6	274 (81)	1.17	2.6	6.7
Oystercatcher	1	0.2	925 (17)	–0.67	0.1	0.1
Bar-tailed Godwit	95	18.7	7447 (43)	0.11	13.9	1.3
Grey Plover	13	2.6	641 (192)	0.44	1.9	2.1
Red Knot	133	26.2	12166 (171)	0.16	19.4	1.1
Redshank	12	2.4	969 (488)	0.33	1.8	1.3
Ruddy Turnstone	27	5.3	1171 (268)	0.76	3.9	2.4
Curlew Sandpiper	7	1.4	1687 (469)	–0.03	1.0	0.4
Ringed Plover	32	6.3	1726 (103)	0.36	4.7	1.9
Sanderling	4	0.8	1676 (223)	–0.22	0.6	0.2
Dunlin	110	21.7	20004 (7737)	–0.33	16.1	0.6
Little Stint	8	1.6	-	-	1.2	-
Terns & Gulls	38	7.5	-	-	5.5	-
Passerines	8	1.6	-		1.2	-

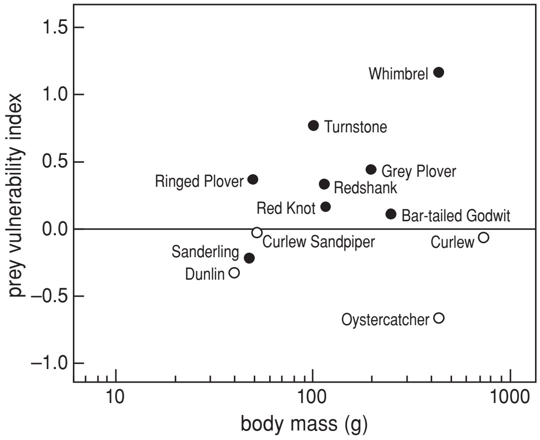

Figure 4.6 Prey vulnerability index as a function of body mass. Bird species are distinguished according to their relative tendency to forage near shorelines (closed dots = close, open dots = far). Little Stint was excluded from this analysis because, due to its tiny size, high tide counts were not reliable. A $\log_{10}$ scale was applied to the x-axis. The prey vulnerability index values are shown in Table 4.2.

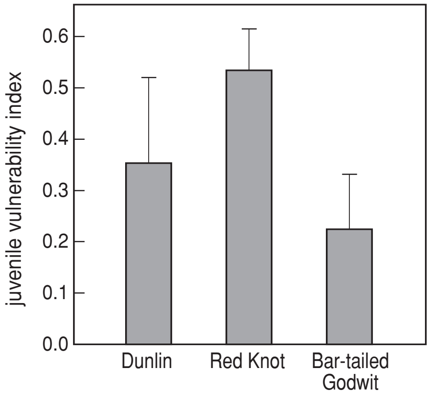

Figure 4.7 Prey vulnerability indices for juveniles, calculated separately for Dunlin, Red Knot and Bar-tailed Godwit. A value of zero would mean that an age-class of a particular species was killed exactly as expected by its relative abundance. The variance around the mean is depicted by error bars (± 1SE).

Table 4.3 Results from survival analyses in MARK, including a correction for overdispersion $\hat{c}$ of 2.127. Φ values refer to average annual survival of Red Knots: Φ_1 = of juveniles in their first year after ringing Φ_2 = of adults in their first year after ringing and 'juveniles' in their second year after ringing; Φ_3 adults two and more years after the year of ringing and 'juveniles' three and more years after the year of ringing. Φ_1 and Φ_3 were used as estimates for juvenile and adult survival respectively. *P* is the resighting probability in a particular year.

Parameter	Estimate	SE	95% confidence interval	
			lower	higher
Φ_1	0.835	0.068	0.657	0.930
Φ_2	0.781	0.040	0.692	0.850
Φ_3	0.889	0.037	0.794	0.944
P_{2003}	0.328	0.052	0.236	0.436
P_{2004}	0.515	0.043	0.429	0.599
P_{2005}	0.484	0.041	0.405	0.563
P_{2006}	0.674	0.053	0.565	0.768

DISCUSSION

The key findings in this study are that: (1) shorebird species were not hunted relative to their abundance at the site, (2) juveniles were clearly overrepresented in raptor kills and (3) direct mortality due to predation accounted for only a small proportion of the annual mortality in the best studied shorebird, Red Knot.

Our observations that three large falcon species were the main predators of shorebirds on the Banc d'Arguin corroborates the study by Bijlsma (1990) on the Iwik peninsula in October 1988. Our calculations of mortality rates due to predation appear closely to cover food requirements of the raptors present. We observed a total bird mass taken per day of 340 g, a close fit to an estimated requirement of 315–483 g, reflecting situations of four (as in 2002, 2004, 2006) or five falcons (as in 2005) present in the area (see Table 4.1).

Attack success by large falcons as reported from several study sites varies considerably, and both Bijlsma (1990) and our study reported remarkably high values of attack success on the Banc d'Arguin (Table 4.4). As raptors preferentially target prey that are easy to catch (Bijlsma 1990, Cresswell & Quinn 2004), we speculate that this high attack success was simply due to the large population of wintering shorebirds always containing vulnerable individuals.

As opposed to large differences in mortalities between age-classes, per-capita mortality of wintering shorebirds on the Banc d'Arguin due to predation by large falcons was low, accounting only for 0.8% of the annual mortality of adult Red Knots

Table 4.4 A review of published estimates of attack success by large falcons hunting on wintering shorebirds.

Location	Surface area (km^2)	Falcon species	N	% Success	Source
Banc d'Arguin, Mauritania	500	Lanner, Barbary, Peregrine	113	30	This study
Banc d'Arguin, Mauritania	500	Lanner, Barbary, Peregrine	32	22	Bijlsma 1990
Boundary Bay, Canada	64	Peregrine	652	14*	Dekker & Ydenberg 2004
Tyninghame, UK	5.5	Peregrine	233	11	Cresswell 1996
Alberta, Canada	30	Peregrine	647	8	Dekker 1988
Alberta, Canada	30	Peregrine	674	8	Dekker 1980
Falsterbo & elsewhere in Sweden	N/A	Peregrine	260	7	Rudebeck 1950-51
Tyninghame, UK	5.5	Peregrine	368	7	Cresswell & Whitfield 1994

* Success rates differed per zone: (1) ocean shore-saltmarsh (44%), (2) the zone extending 0.5 km beyond zone 1 (11%); the zone 0.5 km beyond the salt marsh (10%).

and 6.2% of the annual mortality of juvenile Red Knots. These direct mortality levels are in contrast to studies from the northern temperate zone where predators were observed to kill up to half of the wintering population of shorebirds (Page & Whitacre 1975, Whitfield 1985, Cresswell & Whitfield 1994). Studies of predation may have focused on small and relatively high-risk coastal sites where predation is easy to observe (for an exception see Piersma *et al.* 1993). Two factors may together contribute to this danger, namely distance from cover and flock size (e.g. Quinn & Cresswell 2004). At sites where cover impedes an unobstructed view of the horizon, shorebirds are vulnerable to surprise attacks by predators (Piersma *et al.* 1993, Rogers *et al.* 2006). Foragers with few flock-mates may be at particular risk (Page & Whitacre 1975, Buchanan *et al.* 1988, Cresswell 1994a), because they lack the benefits of flocking, such as increased antipredator vigilance, diluted risk when attacked and the opportunity to confuse predators in co-ordinated escape flight manoeuvres (Barnard & Thompson 1985, Krause & Ruxton 2002, Caro 2005). Quite contrary to the Banc d'Arguin, certain saltmarshes or intertidal flats in small estuaries in the UK (Whitfield *et al.* 1988, Cresswell & Whitfield 1994, Cresswell 1996, Whitfield 2003a, 2003b), the USA (Page & Whitacre 1975) and western Canada (Dekker 1998) demonstrate the above-mentioned risk factors. These estuaries are surrounded by trees, bushes or other topographical structures, which allow stealth attacks: for instance by Sparrowhawks *Accipiter nisus* (in the UK) and Merlins *Falco columbarius* (in the USA and Canada). Correspondingly high mortality rates, biased towards nearshore foragers, were reported from these estuaries (Page & Whitacre 1975, Whitfield 1985, Cresswell & Whitfield 1994). In the Scottish estuary of Tyninghame, Redshanks were 10 times more vulnerable than the shore-avoiding and highly gregarious Red Knot (30–60% against 3–4% of the respective populations were killed in three winter periods, Cresswell & Whitfield 1994), and the same ratio was found in an earlier study on the rocky shore of Scoughal and the estuary of Tyninghame (Whitfield *et al.* 1988). Bolinas Lagoon, California, offers another example of a small sheltered estuary where relatively large numbers of shorebirds were killed (Page & Whitacre 1975, Kus *et al.* 1984). Such high percentages of mortality in a wintering population may be explained by the fact that compared with the Banc d'Arguin, relatively few shorebirds stage in these areas, which may result in a ratio of one raptor to a few hundred or a few thousand shorebirds. On the Banc d'Arguin this ratio is about one raptor to at least 10 000 shorebirds. This low ratio compared with the temperate situation may be explained by the fact that habitat suitability for shorebirds and falcons is governed by different dimensions. Shorebird abundance is limited by the surface area of suitable mudflat, whereas the raptors can never benefit to the full extent from increases in shorebird abundance because for their attacks to be effective they are limited by the linear dimensions of coastline available. That the Banc d'Arguin may already be largely occupied by resident Lanner and Barbary Falcons may explain why the majority of migrating Peregrines appear to skip the Banc d'Arguin as a winter feeding area (Bijlsma 1990, Table 4.1). The open character of the Banc d'Arguin allows shorebirds to avoid surprise attacks by feeding far from cover as long as the tide permits. Yet, some classes of individuals appear to accept higher levels of predation risk by foraging close to cover, and in smaller flocks, even at low tides. This may be due to species-specific foraging characteristics or habitat segregation among age-classes.

First, some species as a rule often find their food alone or in small flocks, close to the shoreline (Table 4.6). For example, Whimbrels are solitary feeders, feeding exclusively on crabs, most of which are Fiddler Crabs *Uca tangeri*, that have a nearshore distribution (Altenburg *et al.* 1982, Zwarts 1990, Zwarts & Blomert 1990, Zwarts & Dirksen 1990). Likewise, Ruddy Turnstones feed in dead seagrass washed ashore, a habit also found by Redshanks and Bar-tailed Godwits, particularly at high tide when mudflats become unavailable. The vulnerability of Ringed and Grey Plovers may not only have been caused by their solitary (territorial) feeding habit (Altenburg *et al.* 1982), but also by the fact that both species stay on sandy shores and on barren sand throughout the tidal cycle, thus creating a large time window for attacks (see also Altenburg *et al.* 1982). Remarkably, Sanderlings, which often feed together with Ruddy Turnstones, and rest together with Ringed Plovers on the barren sand (Altenburg *et al.* 1982, P.J. van den Hout, B. Spaans & T. Piersma pers. obs.), nevertheless seemed not particularly vulnerable (Table 4.6). Secondly, within a species, age-classes may differ in their trade-off between food and danger. Red Knot is a prime example of a species that limits nearshore foraging to times when farshore mudflats are unavailable due to high tide (Piersma *et al.* 1993). Although in our study these shorebird aggregations attracted predators (Fig. 4.4a), encounters per bird hour were fewer, demonstrating the benefit of visiting these nearshore foraging sites in large numbers (Fig. 4.4b). This anti-predator advantage is consistent with the observation that in general the vast majority of Red Knots avoided foraging in small flocks (Table 4.5). Yet, small numbers of juvenile Red Knots did not follow this pattern of predator avoidance, and foraged and rested in nearshore groups of at most a few tens of birds throughout the tidal cycle (P.J. van den Hout unpubl. data - Chapter 5). Similar observations were reported by Van der Have *et al.* (1984) for Dunlin in the Wadden Sea of the Netherlands, in autumn, where the juveniles staged in smaller groups close to the mainland shores. Age-related mortalities in Dunlin in a similar context have been reported by Kus *et al.* (1984). But why would some juvenile Red Knots take these risks? We suggest that competition (see Goss-Custard 1980, Van Gils *et al.* 2004, Van Gils & Piersma 2004, Vahl *et al.* 2005), the currency used to evaluate foraging decisions (Stephens & Krebs 1986) and experience may relegate juvenile individuals to dangerous sites (P.J. van den Hout unpubl. data - Chapters 5 and 6). Cresswell (1994b) observed this in Redshanks in Tyninghame, Scotland. Here, juveniles were excluded from the farshore mussel beds by adults, forcing the former to forage on the saltmarsh where they were nearly five times more likely to be killed by Sparrowhawks. Yet, as energy intake rates on the saltmarsh were higher, adults seemed to consider minimizing predation risk, rather than maximizing intake rate. At least for Red Knot we may have witnessed a similar phenomenon on the Banc d'Arguin. Here, adult birds may exclude juvenile conspecifics from farshore and thus safer foraging areas, causing them to feed along the more risky shoreline habitat (P.J. van den Hout unpubl. data - Chapter 5).

In conclusion, the low mortality rates that we observed on the Banc d'Arguin cannot be used as evidence against the potential importance of predators in shorebird ecology (Lind & Cresswell 2005, Ydenberg *et al.* 2007). Instead, they may reflect the ability of the majority of shorebirds to effectively avoid predation. The relative differences in mortality rates between classes of individuals indicate that non-lethal effects of predation, including enhanced risk of starvation (McNamara & Houston 1994, Houston & McNamara 1999), are probably much more important in moulding patterns of migration and other life-history decisions. At the same time, they demonstrate a strong selection for behaviours such as predator avoidance, foraging strategies and competitive foraging abilities that allow animals to compensate for direct predation risk.

ACKNOWLEDGEMENTS

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BOX III

When shorebirds meet raptors

Along the East-Atlantic Flyway, when foraging on mudflats, non-breeding shorebirds must fear a variety of predators, such as Short-eared Owls *Asio flammea*, Marsh Harriers *Circus aeroginosus*, Hen Harriers *Circus cyaneus*, Goshawks *Accipiter gentilis* and Sparrowhawks, *Accipiter nisus*, and several falcon *Falco* species. For the two most important sites for staging/overwintering (Wadden Sea) and overwintering (Banc d'Arguin) we give an overview of the raptor species these millions of migrant shorebirds, which breed in high Arctic regions, meet on the way. I make an attempt at a crude valuation of the relative impact these may have in terms of disturbance and lethality.

WADDEN SEA

At least on open mudflat, Merlins *Falco columbarius*, which were observed in autumn and winter, hunted primarily passerines and seldom shorebirds (see also Cramp *et al.*, 1983). Hobbies *Falco subbuteo* visit the Wadden Sea in small numbers during their spring and autumn migration (Bijlsma *et al.*, 2001, LWVT/SOVON, 2002). I observed Hobbies creating massive disturbance when hunting smaller shorebirds, such as Dunlins *Calidris alpina* and Ringed Plovers *Charadrius hiaticula*. During our field work Goshawk occasionally traversed open mudflats on passage, but generally created minor disturbance; the same applies to Kestrels *Falco tinnunculus* (I once observed a Kestrel landing on a large wader roost to join shorebirds without causing any disturbance!). Marsh Harriers did cause disturbance among shorebirds, but attacks, let alone catches, were seldom witnessed, at least on open mudflat. Once in a while an Osprey *Pandion haliaetus* visited the Wadden Sea during migration, and, in striking contrast to the Banc d'Arguin (were Ospreys are common all winter and don't instil fear; see below), they created massive disturbance in shorebirds.

But, certainly the most lethal predator of shorebirds in the Wadden Sea is the Peregrine Falcon *Falco peregrinus*. After having recovered from the pesticide crash during the 1960s and 1970s (Ratcliffe, 1993), Peregrines have now become a common raptor in the Wadden Sea. Many Peregrines, particularly from Fenno-Scandia, winter in the Wadden Sea. Numbers mount from August onwards and reach a plateau in mid-winter. Many Afro-Siberian migrants, including Red Knots *Calidris canutus*, evade these raptor peaks by migrating just before (autumn) or after (spring). Yet, juveniles, by migrating later in autumn, experience higher overlap with raptors (Figure III.1). Similar patterns were reported by Lank *et al.* (2003), Ydenberg *et al.* (2005) and Ydenberg *et al.* (2007). But as virtually all sand bars and spits contain one or more Peregrines during winter, shorebirds that spend the winter in the Wadden Sea are regularly confronted with these fast aerial hunters.

Peregrines were most often seen hunting in early morning and just before dark. They were highly selective towards 'easy' prey, such as exhausted and/or lost racing pigeons, or – often nocturnal – migrants that were slow flyers (such as Rails *Rallus* species) and/or not familiar with the mudflat habitat (forest species, pelagic species). Such hunting comfort, which relaxed predation pressure for shorebirds, only presented itself at times of migration or in weekends (racing pigeons) (van den Hout, 2009).

BANC D'ARGUIN (MAURITANIA)

Several raptor species occur at Banc d'Arguin. During our field work some raptors visited Banc d'Arguin occasionally on migration, such as some eagle species (Bonelli's Eagle *Hieraaetus fasciatus* and Golden Eagle *Aquila chrysaetos*), but these

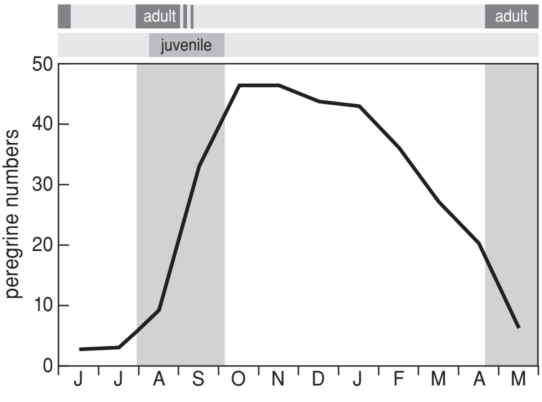

Figure III.1 How transient Red Knots avoid the peak of Peregrine migration by travelling early and late in the season. The bars represent the staging periods in the Dutch and German (the latter particularly in spring) Wadden Sea of *C. c. canutus*. The dashed portion of the dark grey bar represents the period in which a minority of the adult Red Knots are still present in the Wadden Sea. The pattern of Peregrine occurrence refers to the Dutch Wadden Sea and is based on counts in 1989-2006. Peregrine numbers are 40% imputed. Adapted from Van den Hout, 2009.

were mostly seen resting. Black Kite *Milvus migrans*, and Montagu's Harrier *Circus pigargus* occur more than occasionally during migration, but were still uncommonly seen. Conversely, Marsh Harriers were common in winter. They were usually seen in slow flight checking dune ridges, stopping every now and then. Shorebird disturbance, however, was commonly limited to a small zone created by the harrier's flight path, whereas attacks on shorebirds were seldom witnessed (however, in view of their hunting style, attacks may be easily concealed from the observer!). Marsh Harriers were often seen at places were shorebirds gathered in large numbers, such as high tide roosts. Occasionally a Marsh Harrier was spotted hanging around falcons on the hunt in order to steal their prey – in which they sometimes succeeded. Short-eared Owls were occasionally spotted in the low dunes bordering the mudflat, but neither attack nor disturbance of shorebirds was ever witnessed. Ospreys were common. One or more Ospreys were commonly spotted while resting close to roosting shorebirds. Quite contrary to the situation in the Wadden Sea (as just described) shorebirds were by no means disturbed by Ospreys, even when they flew very close overhead!

Clearly, the raptors that stroke most terror into shorebirds at Banc d'Arguin were falcons *Falco* spp.. Although many shorebirds that winter in Africa may succeed in escaping the peak number of Peregrines in the Wadden Sea, they are still confronted with falcons after arriving on their winter destination. Here they encounter at least three species of large falcons: Peregrines, either transients in autumn, or wintering individuals, and at least two resident species: Lanner Falcon *Falco biarmicus*, and Barbary Falcon *Falco pelegrinoides*. The plumage characteristics of Barbary Falcon that occur at Banc d'Arguin seem intermediate between populations from the Middle East and a subspecies of Peregrine, *Falco peregrines brookei*. These birds represent the most westerly extreme of the Barbary Falcon cline. In fact, Barbary Falcon was long considered a subspecies of Peregrine (*Falco peregrines pelegrinoides*), and traces of *F. p. brookei* which occurs in the south of France, Spain and coastal North Africa East through Mediterranean to Caucasus may be apparent in these falcons, which may cause the large variation in plumages among these falcons (Cramp *et al.*, 1983, van Duivendijk, 2002, Isenmann, 2006, Forsman, 2007; Fig. III.2).

At Banc d'Arguin falcons are most abundant in autumn, when both transient and resident birds are present. Like in the Wadden Sea, at this time of the year, predation on shorebirds was invariably relaxed when falls of passerine migration brought many exhausted passerines – most often Pied Flycatchers *Ficedula hypoleuca* – inland.

In our study area the resident falcons staid all winter, but their numbers decreased markedly in spring. I speculate that these birds leave foraging sites closer to mainland and possibly withdraw on remote islands were they can safely breed free from Golden Jackal *Canis aureus*. Indeed, breeding of Lanner Falcon was reported on remote islands at Banc d'Arguin; eggs are laid between early February and early May, and fledging takes place between early April and early May (Cramp

Figure III.2 Falcon species that occur on the Banc d'Arguin. (A) Lanner Falcon *Falco biarmucus erlangeri* (adult); picture taken by Jeroen Reneerkens; (B) Barbary Falcon *Falco pelegrinoides* (adult); picture taken by Jan van de Kam (C) Lanner Falcon (subadult); picture taken by Jan van de Kam (D) Peregrine Falcon (picture not taken at Banc d'Arguin, but in Sitz Mountains, Alaska, by Piet J. van den Hout).

et al., 1983, Isenmann, 2006). So, the danger of jackals for Lanner eggs (or the incubating owner of these eggs) might relax predation danger exactly at times when shorebirds become more vulnerable for predation as they fuel up for northward migration (see also Chapter 5).

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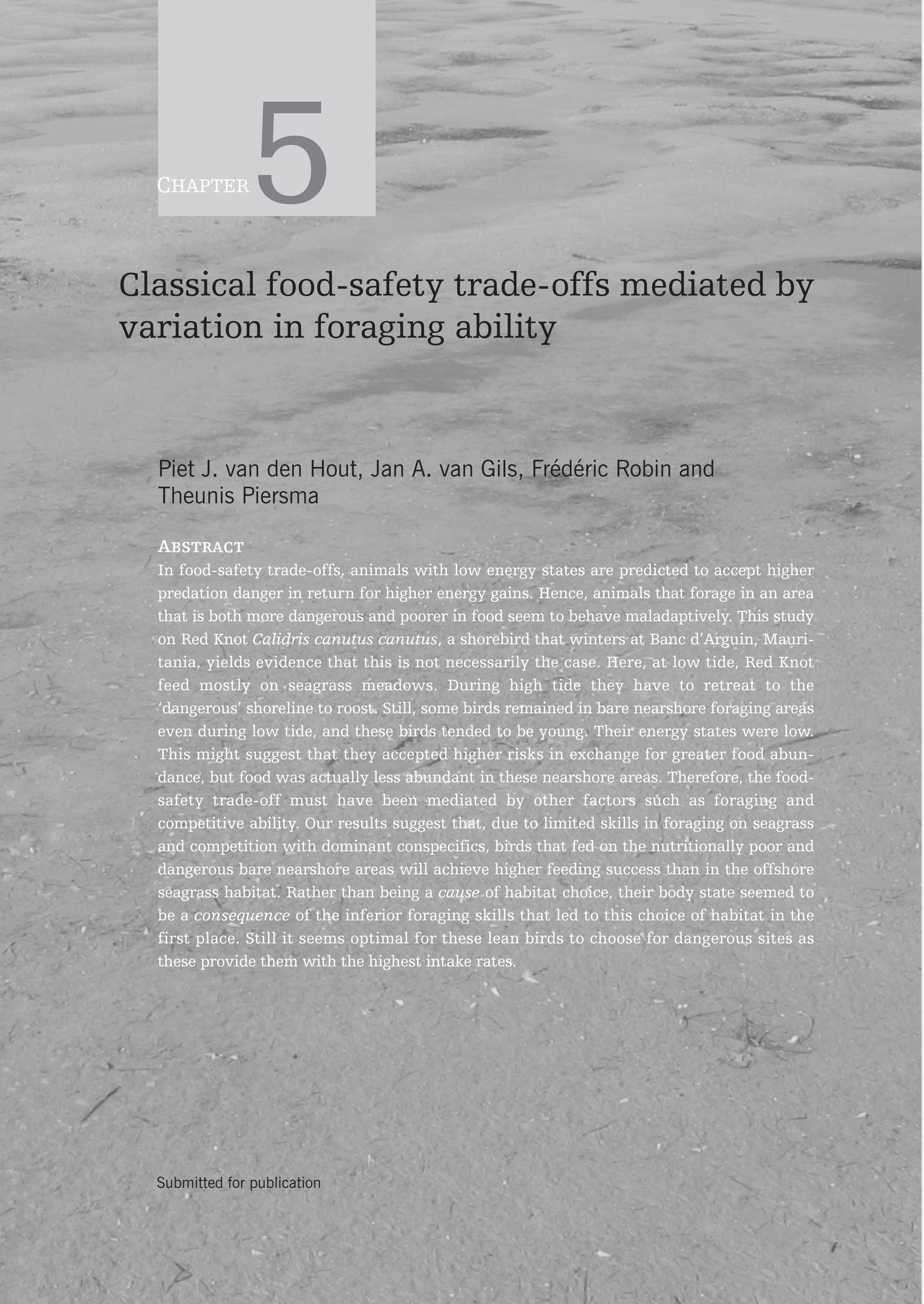
I am grateful to Arend Wassink for sharing his ideas about – intergrades between – Peregrine and Barbary Falcon in North-West Africa.



CHAPTER 5

Classical food-safety trade-offs mediated by variation in foraging ability

Piet J. van den Hout, Jan A. van Gils, Frédéric Robin and
Theunis Piersma

ABSTRACT

In food-safety trade-offs, animals with low energy states are predicted to accept higher predation danger in return for higher energy gains. Hence, animals that forage in an area that is both more dangerous and poorer in food seem to behave maladaptively. This study on Red Knot *Calidris canutus canutus*, a shorebird that winters at Banc d'Arguin, Mauritania, yields evidence that this is not necessarily the case. Here, at low tide, Red Knot feed mostly on seagrass meadows. During high tide they have to retreat to the 'dangerous' shoreline to roost. Still, some birds remained in bare nearshore foraging areas even during low tide, and these birds tended to be young. Their energy states were low. This might suggest that they accepted higher risks in exchange for greater food abundance, but food was actually less abundant in these nearshore areas. Therefore, the food-safety trade-off must have been mediated by other factors such as foraging and competitive ability. Our results suggest that, due to limited skills in foraging on seagrass and competition with dominant conspecifics, birds that fed on the nutritionally poor and dangerous bare nearshore areas will achieve higher feeding success than in the offshore seagrass habitat. Rather than being a *cause* of habitat choice, their body state seemed to be a *consequence* of the inferior foraging skills that led to this choice of habitat in the first place. Still it seems optimal for these lean birds to choose for dangerous sites as these provide them with the highest intake rates.

Submitted for publication

INTRODUCTION

Habitat selection forces animals to choose among locations that differ in many aspects (Piersma, 2006), but the potential for energy gain and relative predation danger are usually singled out as being the most important (van Gils *et al.* 2004). It has been empirically demonstrated (reviews by Lima & Dill 1990, Lima 1998, Brown 1999, Brown & Kotler 2007, Cresswell 2008), and it has been made theoretically plausible (Houston & McNamara 1999; Houston *et al.* 1993; McNamara *et al.* 2005), that individuals are capable of responding in adaptive ways to trade-offs between energy gain and safety from predators, trade-offs that may be mediated by the energy state of the animal (Real & Caraco 1986, Barnett *et al.* 2007, Kotler *et al.* 2010). Due to the balanced effects of competition, safety-in-numbers and habitat choice by their own predators, foragers are generally considered to trade rich and risky feeding opportunities against poor and safe options (Hugie & Dill 1994, Moody *et al.* 1996, Sih *et al.* 1998, Bednekoff 2007).

Nevertheless, it is not always clear why individuals differ in habitat choice. For instance, young birds are often found segregated from the principal flocks, in roosting or foraging areas that would rarely be visited by adult conspecifics, usually because these areas are more dangerous (Swennen 1984, van der Have *et al.* 1984, Cresswell 1994b). Are such foraging decisions to be considered as trade-offs, or are they merely driven by constraints such as inferior abilities in competition or foraging? Clearly, foraging decisions that entail more predation danger must be compensated by food in order to be considered adaptive. As an example, Cresswell (1994b) found that although juvenile Redshanks *Tringa totanus* were driven off the safest foraging areas by dominant adults, they were nevertheless compensated by higher food abundance in the more dangerous feeding areas. Cresswell proposed that these juveniles decided to maximise energy intake at the expense of safety, whereas adult Redshanks maximised safety at the expense of food. But what if individuals forage in places that are both more dangerous ánd poorer in food? One may be inclined to consider this as maladaptive behaviour. Yet, few studies have actually studied the mechanisms underlying such habitat choices.

In fact, trade-offs may be mediated by factors such as an ability to forage and to compete, which for immature birds may lead to situations in which they simply cannot afford to feed in places that are either safest from predators, or richest in food (Goss-Custard & Durell 1983, Cresswell 1994b, Minderman *et al.* 2006). Several studies on shorebirds indicate that age-differences in foraging skills can persist quite some time, including the period after arrival in their winter quarters (Groves 1978, Burger 1980, Espin *et al.* 1983, Goss-Custard & Durell 1987a). Such differences are expected to be most pronounced in species that have specialized and sophisticated feeding methods that take time to learn (Wunderle 1991). As demonstrated in Eurasian Oystercatchers *Haematopus ostralegus*, adults may retard the rate at which juveniles acquire foraging proficiency on the most profitable prey types because they compete with immatures (Goss-Custard & Durell 1983). The latter can

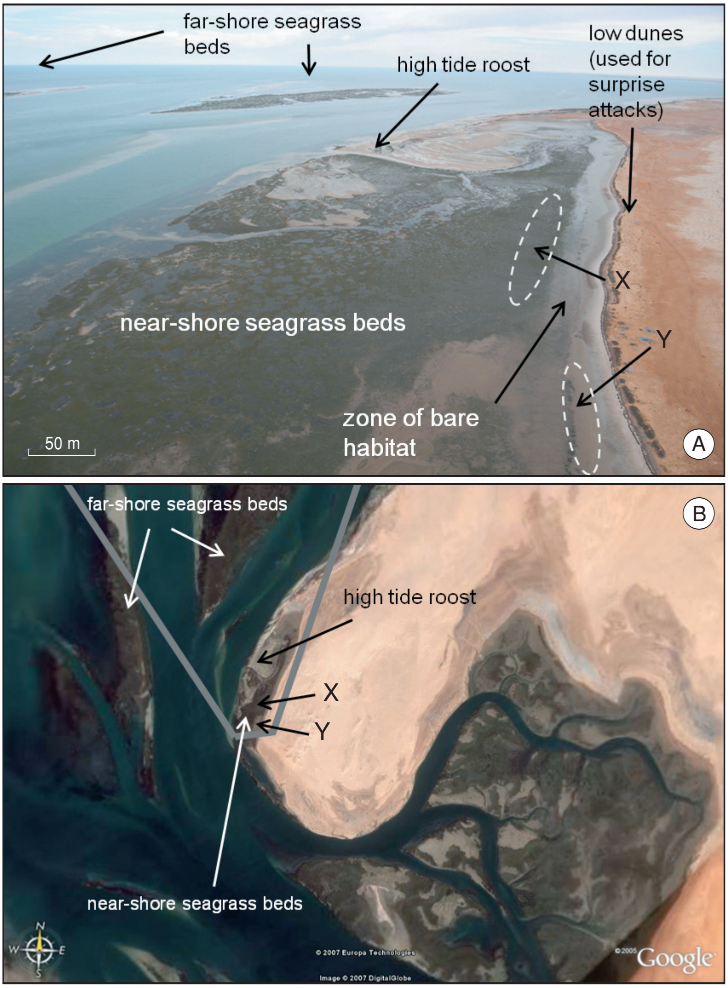


Figure 5.1 Study site, depicting micro-habitat types, i.e. bare habitat, particularly in a nearshore zone, and seagrass habitat, starting further from the shoreline, as seen from a height of 150 m from the south (A) and on a map (B). The grey angle in B corresponds to the viewpoint in A. Locations X (seagrass habitat) and Y (bare habitat), where agonistic interactions were recorded, are shown. Photo courtesy by en Haut! M. Broquère - S. Nancy.

only begin to eat mussels when they have sufficiently matured to compete with adults on the mussel beds. Thus, abilities in foraging and competitiveness may interact and mediate trade-offs between safety and food.

On the Banc d'Arguin, Mauritania, a major wintering site for shorebirds along the East-Atlantic Flyway (Altenburg *et al.* 1982, Smit & Piersma 1989, Zwarts *et al.* 1998, Davidson & Stroud 2006), there are sharp transitions between intertidal areas covered with seagrass and areas that are bare (Honkoop *et al.* 2008; see Fig. 5.1). With respect to small bivalves ingestible by shorebirds (Zwarts & Wanink 1993), seagrass habitat is more than twice as rich in biomass as bare habitat (Honkoop *et al.* 2008). Food availability may be one of the reasons why Red Knots *Calidris canutus canutus* generally feed on seagrass and largely avoid the bare sandflats (Altenburg *et al.* 1982, Engelmoer *et al.* 1984; personal observation).

Surprisingly, the nearshore bare zones are regularly visited by small flocks of Red Knots, mainly juveniles (van den Hout *et al.* 2008). This is more remarkable as

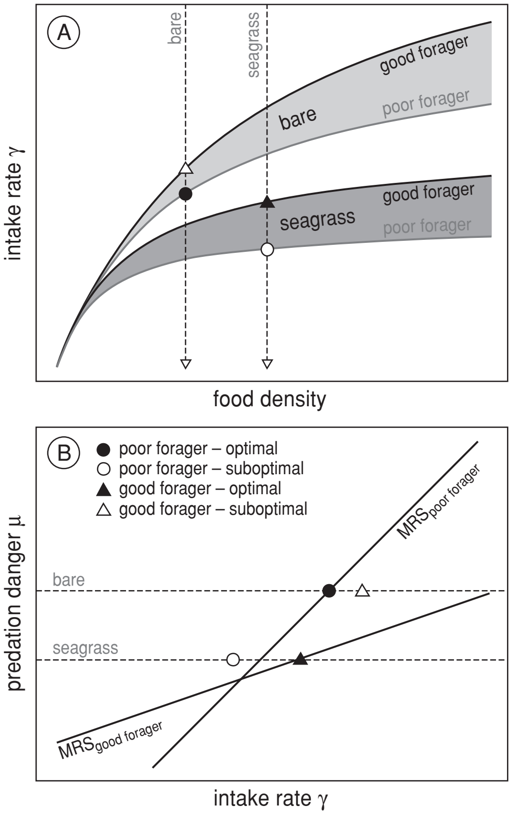


Figure 5.2 (A) Graphical illustration of Holling's type II functional response curves for poor and good foragers in bare and seagrass habitat. Searching efficiency is expected to be lower in seagrass (flatter slope than in bare) and handling time longer (lower asymptote than in bare). Therefore, birds can achieve higher intake rates in bare despite a lower food density. But foragers differ in searching and handling proficiency, resulting in differences in intake rate within the same habitat. Legend in (B) applies to both panels. (B) State space illustrating the predicted different optimal decisions by poor and good foragers with respect to the trade-off between energy intake γ and predation danger μ (adapted from Houston & McNamara, 1999). In this state space, fitness is maximized in the lower right corner of the graph (where predation danger μ is lowest and intake rate γ is highest). Which of the two available options (seagrass or near-bare) is located "lowest right" depends on a bird's marginal rate of substitution (MRS) of predation danger for energy intake. Birds in a poor energy state (usually being poor foragers) experience high MRS and should therefore feed in the nearshore bare habitat. In contrast, birds in a high energy state (usually being good foragers) experience low MRS and should therefore feed in the seagrass habitat.

predation danger in these patches is particularly high: shorebirds on the Banc d'Arguin have to fear large falcons (Peregrine *Falco peregrines*, Lanner *Falco biarmicus* and Barbary Falcon *Falco pelegrinoides*) which restrict their hunting to the mainland coasts (van den Hout *et al.* 2008). Low dunes bordering the mudflats are used by these raptors to conceal their approach. We suspect that the strong bias towards juvenile mortality in Red Knots (van den Hout *et al.* 2008) relates to this danger. Here we ask ourselves why any Red Knot would take such risks.

Compared with the 'sorted' soft sediments characteristic of most of the western European coastline (Piersma *et al.* 1993, Bocher *et al.* 2007), intertidal seagrass meadows are a complex habitat (Gotceitas & Colgan 1989, Harris *et al.* 2004, Horinouchi *et al.* 2009). Food items can either be found between the seagrass roots, or in the muddy substrate underneath the layer of roots (Altenburg *et al.* 1982; personal observation). Outside the tundra breeding areas, Red Knots feed mostly on hard-shelled invertebrates extracted from soft wet sediments (Piersma 2007). They find these prey by an apparently unique 'remote sense' to detect hard-shelled items in soft sediments (Piersma *et al.* 1998). Red Knots have been found to obey the assumptions of the functional response as described by a Holling disc equation (Holling 1959a), i.e. that intake rates increase with prey density, but level off as they become constrained by handling time (Piersma *et al.* 1995). We suspect that the complexity of the seagrass habitat challenges a Red Knot's searching and handling abilities (Fig. 5.2A). For inexperienced birds such difficulties may be aggravated by interference competition with dominants (Goss-Custard *et al.* 1977, Caldow *et al.* 1999). Therefore, due to differences in foraging and competitive abilities, we predict differences between good and poor foragers in the trade-off between energy gain and safety from predators, such that good foragers can afford to forage on the structurally complex seagrass areas where they are relatively safe from predators, while poor foragers should forage in 'easier' nearshore bare habitat accepting higher predation danger (Fig. 5.2B). The latter is because they can achieve higher intake rates in bare areas, despite lower food abundance.

In the context of trade-offs between food and safety we will test our predictions by comparing habitat use of young and old birds in (a) nearshore bare foraging sites very close (0–40 m) to raptor-concealing cover, and (b) seagrass beds that lie between 40–250 m from shoreline cover. Additionally, to underpin the idea that there may be age-related differences in competitiveness, we quantify age-related agonistic behaviour.

METHODS

Study site and standard observation procedures

The Banc d'Arguin is an area of shallow water, islands and intertidal sand- and mudflats that stretches along the northern coast of Mauritania, bordering the Sahara desert from about 20°50'N, 16°45'W to 19°20'N, 16°28'W. The Parc National du Banc d'Arguin covers an area of 12 000 km^2 of sea, shoreline and desert, 500 km^2 of which are intertidal. Both the intertidal flats and parts of the shallow sea bottom of Banc d'Arguin are dominated by vast seagrass beds, mainly *Zostera noltii* on the intertidal flats (Altenburg *et al.* 1982, Wolff and Smit 1990, Isenmann 2006). The central part of the peninsula consists of barren, up to 15 m high hills used by the falcons as resting and eating places. The fieldwork was carried out on the Iwik peninsula (19°53'N, 16°17'W) in autumn/winter periods of 2002/2003 through 2007/2008, and in spring 2005.

Each winter we trapped shorebirds with mist-nets during calm nights around New Moon when high tide levels are highest (van den Hout *et al.* 2008). The captured Red Knots were weighted and age was determined. Age (juvenile or adult) was determined, both in the hand and in the field, on the basis of plumage characteristics. Juvenile birds are characterised by their whitish under-parts with pink-buff wash and greyish brown upperparts; the coverts have pale fringes and dark sub-terminal lines (Prater *et al.* 1977). Although these characteristics gradually faint in the course of winter, some inner grey-brown coverts with sub-terminal bars remain. Even when these bars have been lost the brownish coverts are distinctive.

Predation danger

As raptors as a rule rely on opportunities to catch their prey unawares, habitat structures that conceal approaches of attacks contribute significantly to predation danger by increasing the lethality of attack (Dekker 1980, Whitfield 1985, Cresswell 1994b, Hilton *et al.* 1999a, Whitfield 2003a, Dekker & Ydenberg 2004, Cresswell and Whitfield 2008, Cresswell *et al.* 2010). Following Lank and Ydenberg (2003), we use danger to indicate the combination of predator abundance and habitat structure (i.e. it is essentially an attribute of the environment) and risk to indicate the actual probability of being depredated, a property that is also affected by anti-predation measures of the prey themselves.

In order to investigate whether being in close proximity to the dunes (the obstructive cover of approaching falcons on the hunt), was indeed perceived as dangerous, we examined vigilance behaviour by foragers. We recorded the number of head-ups per min with respect to distance from cover and flock size. This 'head-up' vigilance was defined as the raising of the head from head-down foraging to at least a horizontal position (Metcalfe 1984). We used these estimates of danger to distinguish dangerous and safe foraging zones.

Food availability, food intake and diet composition

We collected benthos samples from random sites across our study area, including both bare and seagrass-covered habitats. We collected 44 samples from the seagrass (8 in December 2003, 11 in December 2004, 18 in April 2005 and 7 in November 2006), and 27 samples from bare habitat (18 in December 2003, 1 in December 2004, and 8 in April 2005). Samples were taken by a sediment core (1/56 m^2) that was inserted in the sediment to a depth of 20 cm. To distinguish accessible from inaccessible prey (Red Knots have a bill length of 3–4 cm), the top layer (0–4 cm) was separated from the bottom layer (4-20 cm). Both layers were subsequently sieved over a 1-mm mesh. All prey remaining on the mesh were stored frozen for later analysis. Each prey was identified to species and size. Below we restrict our analyses to the fraction of bivalves available to Red Knots. Prey are considered to be available if they are both accessible (i.e. living in the top layer of the sediment) and ingestible (i.e. not too large to prevent swallowing whole) (Zwarts & Wanink, 1993). With respect to the latter, maximal ingestible lengths were calculated based on a gape circumference limit of 30.6 mm for Red Knots (Zwarts & Blomert 1992).

As is standard usage in analyses of bivalves as food for Red Knots (Dekinga & Piersma 1993, van Gils *et al.* 2003, 2005a), we determined metabolizable energy content and the amount of indigestible shell mass by separating the meat from the shell. Subsequently we dried both flesh and shell to constant mass in a ventilated oven at 55-60ºC. Shell mass was then weighed to the nearest 0.001 g using an electronic balance. The dried flesh was incinerated at 550ºC for two hours, after which ash free dry mass of the flesh ($AFDM_{flesh}$) was determined by weighing to the nearest 0.001 g on an electronic balance. Metabolizable energy content of the flesh was further calculated as $AFDM_{flesh}$ × energy density × assimilation efficiency. The latter two were assumed to be constant at respectively 22 kJ/g $AFDM_{flesh}$ (Zwarts & Wanink 1993) and a factor 0.8 (van Gils *et al.* 2005a). For small bivalves and gastropods that did not allow separation of flesh and shell, dry mass and ash-free dry mass were determined of entire specimens; species-specific correction factors were used accounting for organic matter residing in the hard parts (van Gils *et al.* 2006a), and the loss of carbon in the incineration process. Prey quality, a major determinant of a knot's achievable daily intake rate under a digestive constraint (van Gils *et al.* 2003, van Gils *et al.* 2005b, c) is the ratio between metabolizable energy content and indigestible shell mass (J metabolizable energy g^{-1} shell mass; van Gils *et al.* 2005a).

Energy intake rates were estimated by direct observation of swallowed prey items using a 20–60× zoom spotting telescope. Droppings were used to verify the species composition, sizes and mass values of ingested prey items. At places where we had observed Red Knots to forage for at least half an hour we collected samples of 50 droppings (13 samples were from bare and 23 samples from seagrass areas). These samples were stored frozen upon time of analyses. Using a binocular microscope we identified species and sorted them out to weight fractions. By using the species-specific relationships between hinge and umbo (the rounded apex of a bivalve) to length as derived from entire specimens, we could deduce the length classes of specimens in the diet of birds, their energetic values, the indigestible shell mass involved, and thus prey quality (Dekinga & Piersma 1993, van Gils *et al.* 2005a). We calculated instantaneous energy intake rates (mg $AFDM_{flesh}$ /s) using the combination of item intake rates and average energy equivalents of the prey as deduced from the dropping analyses.

Age distribution

We examined age-composition across the tidal cycle in randomly encountered flocks in bare and seagrass areas, the first always found within 40 m from the shoreline cover, the second 40–250 m from the shoreline and hence the predator-concealing dunes (see Fig. 5.1). Estimates of food, agonistic interactions, and the birds' energy state were taken from the same two habitat zones. In the final stages of incoming tide, when birds were gathering in high numbers at high densities, juvenile percentages were often estimated from subsamples of flocks, and consequently flock sizes are generally underestimated for this period.

Energy states

As demonstrated for geese (Black *et al.* 2007) and for Red Knots (Wiersma & Piersma 1995, van Gils *et al.* 2006a), useful estimates of body mass and fat load can be obtained by visual inspection of abdominal profiles. We assessed abdominal profile indices (API's) of individuals in a range from 1 (very lean) to 5 (very fat) (Wiersma & Piersma 1995) with a 20–60× zoom spotting telescope from the shoreline during various stages of tide cycle and at various distances from obstructive cover.

Agonistic interactions

To get information about competitive interactions between adult and juvenile Red Knots, we studied flocks crowding in nearshore habitat in the final stage of the low water period between 10–25 October 2006. We conducted 92 group scans (Martin & Bateson 1993) at locations X and Y where birds foraged on seagrass and on bare sandflat respectively (Fig. 5.1). Scans of 5–10 min were made by moving the telescope, at 20× magnification, from one side to the other at slow pace. We had no indication whatsoever that the birds were disturbed by our presence. We recorded the direction of aggressive displacements (adult displacing juvenile, or *vice versa*, and adults or juveniles displacing members of their own age group). We thus described each interaction in terms of age of the contestants (adult, juvenile or uncertain). Observed aggressive displacements between classes of individuals (adult-adult, juvenile-juvenile, adult-juvenile) were compared with predicted ones under the assumption of an absence of age bias using the numbers of adult and juvenile birds tallied to be present (Groves 1978). For a mixed flock of adults and juveniles of any specified composition:

p = number of adults / (number of adults + number of juveniles)
q = number of juveniles / (number of adults + number of juveniles)

Thus, the expected frequencies of aggressive interactions, when interactions occur between random individuals, are p^2 and q^2 for aggression among adults and juveniles respectively, and $2pq$ for adult over juvenile and juvenile over adult interactions. We calculated the relative probabilities of age-specific displacement events using the following equation:

$$P_{\text{attack}} = P_{\text{encounter}} \times P_{\text{attack}|\text{encounter}}$$

For all 92 group scans and each possible type of interaction the directions of deviations from expected frequencies were counted and evaluated by the sign test (Groves 1978, Zar 1999).

STATISTICAL ANALYSES

All statistical analyses were performed using the R package (version 2.9.0). All mean values are presented with standard errors. Assumptions of normality and homoscedasticity were tested by the Shapiro-Wilk test and F-test respectively (Zar 1999, Crawley 2007). Wilcoxon rank-sum tests, which were applied as a non-parametric alternative for the t-test for independent samples, were performed with continuity correction of 0.5 (Zar 1999).

RESULTS

Predation danger

The frequency of head-ups confirmed that close to shore Red Knots were most vigilant, and that they thus seem to perceive the nearshore bare areas as the most dangerous (Fig. 5.3), and this result remained when correcting for flock size (GLM on ln-transformed data, Distance from cover: $t = -8.9$, $P < 0.001$; Flock size: $t = -3.2$, $P = 0.002$). Flock size correlated with distance from shore (Pearson's product-moment correlation, $t = 7.6849$, $df = 350$, $P < 0.001$).

The rate of scanning the environment dropped quickly after a distance of approximately 40 m. On this basis 40 m was considered a biologically meaningful threshold distance between a relatively dangerous and a relatively safe zone, a distance from shore that fortuitously coincided with the transition between bare and seagrass habitat.

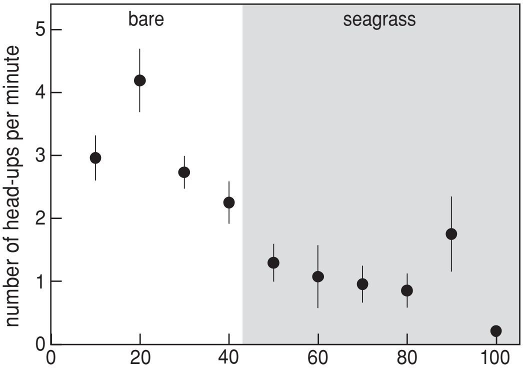


Figure 5.3 Head-up frequency as a function of distance from cover in Red Knots observed near Iwik on Banc d'Arguin in autumn/winter periods of 2002/2003 through 2007/2008, and in spring 2005.

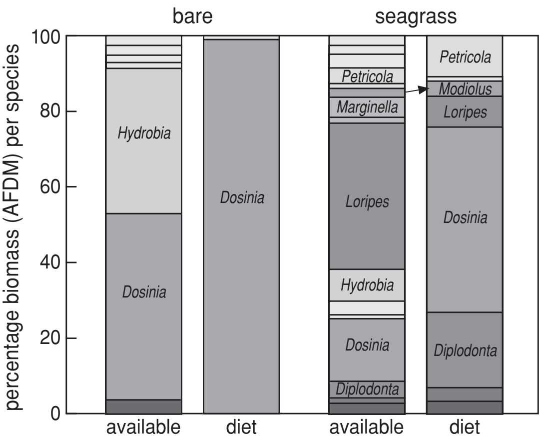


Figure 5.4 Available food density and diet composition in bare and seagrass habitat, expressed in percentages of species in terms of biomass (AFDMflesh). Only the numerically most important species are named.

Food availability, food intake and diet composition

Biomass densities (g $AFDM_{flesh}$ m^{-2}) were higher in nearshore seagrass beds (3.46 ± 0.62 g $AFDM_{flesh}/m^2$) than in nearshore bare areas (1.71 ± 0.45 g $AFDM_{flesh}/m^2$; Welch Two Sample t-test, t = 2.2697, df = 68.711, $P = 0.026$).

Red Knots foraging on the bare sandflat selected a single species of bivalve (*Dosinia hepatica*; Fig. 5.4), whereas in the more food-diverse seagrass areas, several species of mollusk were eaten in quantity (Fig. 5.4). The quality of available mollusk prey was higher in seagrass areas (1.85 ± 0.08 kJ/g dry $mass_{shell}$) than in the bare sandflats (1.30 ± 0.29 kJ/g dry $mass_{shell}$; Wilcoxon rank-sum test, $W = 34075.5$, $P < 0.001$); this difference was even greater when calculated for actually consumed prey (Fig. 5.4; weighted sums: 1.96 kJ/g dry $mass_{shell}$ in seagrass vs. 0.79 kJ/g dry $mass_{shell}$ in bare).

Overall intake rates (mg $AFDM_{flesh}/s$) were higher in seagrass areas than on the bare sandflat (0.31 ± 0.01 vs. 0.27 ± 0.01 mg/s; t = 2.5856, df = 723.949, $P = 0.010$). Despite the lower available food density, juveniles on the bare sandflat tended to achieve higher intake rates than juveniles on seagrass (0.25 ± 0.02 vs. 0.20 ± 0.03 mg/s; t = –1.6859, df = 63.528, $P = 0.097$). Conversely, adult birds in seagrass habitat did not achieve higher intake rates than adult birds in bare habitat (0.32 ± 0.02 vs. 0.29 ± 0.02 mg/s; t = 1.3573, df = 284.852, $P = 0.176$). However, adult birds clearly achieved higher intake rates than juveniles in both seagrass ($W = 7390.5$, $P < 0.001$) and bare areas ($W = 9493.5$, $P = 0.006$) (all values are summarized in Table 5.1).

Age-distribution

Around high, as well as around low tide, the percentage of juveniles in a flock in nearshore bare habitat (0–40 m from cover) exceeded the overall percentage of 24% found in mist net catches (Fig. 5.5). In the hours around high tide 77.6 ± 4.7% of the nearshore knots were juvenile, and during low tide 66.3 ± 6.0% were juvenile (both

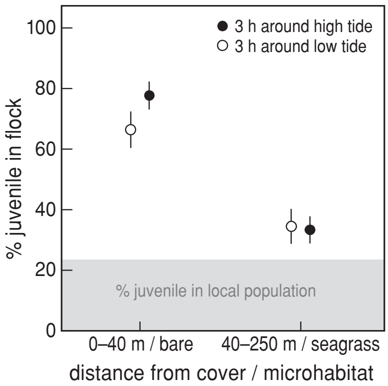


Figure 5.5 Percentage of juvenile Red Knots 3h around low tide and 3h around high tide in autumn/winter periods of 2002/2003 through 2007/2008, and in spring 2005.

estimates yielded *P*-values < 0.001 for the comparison with the population average of 24%, based on z-values from a standardized normal distribution). On seagrass 40–250 m from cover, juvenile percentages were as low as 33.4 ± 4.7% around high tide and 34.1 ± 5.9% during low tide. Although these values were significantly lower than in bare area ($t = 7.4071$, $df = 185.121$, $P < 0.001$ – data were arcsine-square-root transformed prior to analysis), they still exceeded the population estimate of 24% (*P*-values, based on z-values from a standardized normal distribution, are 0.023 for high tide, and 0.044 for low tide). In nearshore bare habitat, the percentage of juveniles tended to increase around high tide ($t = –1.6886$, $df = 70.472$, $P = 0.096$), whereas for seagrass tidal stage was not related to juvenile percentages ($t = –0.1261$, $df = 96.679$, $P = 0.900$; Fig. 5.5).

Flock sizes were much smaller in nearshore bare than in seagrass habitat (Wilcoxon rank-sum test, $W = 2109.5$, $P < 0.001$). Flock sizes on bare were similar at all tides ($W = 621$, $P = 0.105$), while flock sizes in seagrass beds were higher around high tide ($W = 2136$, $P = 0.002$). These high tide flock sizes were obviously caused by birds approaching the shore at times offshore foraging areas became submerged by the tide.

Table 5.1 Overview of intake rates (in mg s^{-1} ash-free dry mass of meat, $AFDM_{flesh}$) in nearshore bare habitat compared to nearshore seagrass habitat. An asterisk stands for significance ($P < 0.05$).

	Bare	Seagrass	*P*-value bare vs. seagrass
All	0.27 ± 0.01	0.31 ± 0.01	0.010 *
Adult	0.29 ± 0.02	0.32 ± 0.02	0.176
Juvenile	0.26 ± 0.02	0.20 ± 0.03	0.097
P-value adult vs. juv	0.006 *	<0.001 *	

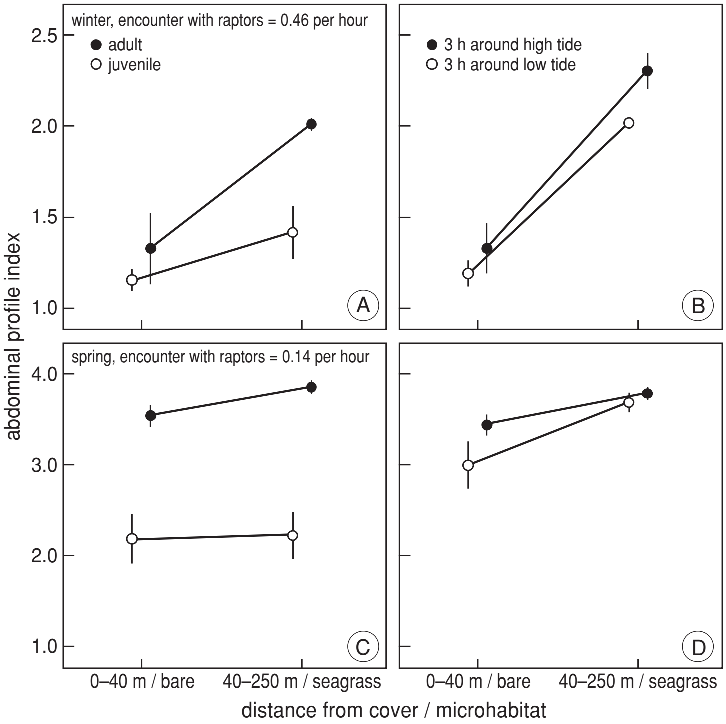


Figure 5.6 (A) Abdominal profile indices of adult and juvenile Red Knots as a function of two distance classes from cover (0–40 m and 40–250 m), in winter, with mean ± SE raptor encounter probability of 0.46 ± 0.12 raptors h^{-1}. (B) API's in winter for two distance classes from cover (0–40 m and 40–250 m), 3 h around high and 3 h around low tide, in winter. (C) The same as (A), but in spring, with raptor encounter probability of 0.14 ± 0.05 raptors h^{-1}. (D) The same as (B), but in spring.

Energy state

Winter (November-December) body masses of juveniles (118.3 ± 0.5 g; range 84–152) were significantly lower than of adults (125.8 ± 0.33 g; range 99–152 g; Welch Two Sample t-test, $t = -2.709$, $df = 469.4$, $P = 0.007$). Adult body masses were higher in April (149.51 ± 2.42 g; range 114–183 g), due to fattening for northward migration (Piersma & van Brederode 1990). Note that this was not so for juveniles (117.65 ± 2.41 g; range 97–147 g) that do not migrate to breeding grounds in their second calendar year (van Dijk *et al.* 1990). Hence, inescapably, body mass differences between these age-classes were greater in spring ($t = -9.3127$, $df = 51.485$, $P < 0.001$).

In winter, abdominal profiles of nearshore foragers were lower than those of offshore foragers (Wilcoxon rank-sum test, $W = 915.5$, $P < 0.001$; Figs. 6A and B) and those of juveniles were lower than those of adults (Wilcoxon rank-sum test, $W = 6042$, $P < 0.001$; Fig. 5.6A). In spring, juveniles that foraged near the shore had similar abdominal profiles as juveniles that fed on seagrass away from the shore ($W = 81$, $P = 0.89$; Fig. 5.6C).

However, the abdominal profiles of adults and juveniles approaching the shoreline in spring were higher than in winter (Fig. 5.6C,D vs 5.6A,B), but the pattern that nearshore foragers had lower abdominal profiles than offshore foragers remained in adults (Wilcoxon rank-sum test, $W = 4165.5$, $P < 0.006$), although the difference was smaller than in winter (9.3% in spring vs. 51.5% in winter).

Agonistic interactions

Depending on the stage of tide, the total area that we scanned for birds varied between 50 and 400 m^2. Locations X (the seagrass patch) and Y (the bare patch) strongly differed in age-distribution: relatively more juveniles assembled at area Y in which they represented on average 69% of a flock, whereas at location X on average 39% of the Red Knots were juvenile (Table 5.2). Despite this difference in age-distribution, at both locations age-related aggression patterns were similar (Table 5.2). A sign test revealed that all the interactions involving juveniles revealed more aggressive interactions than expected from encounter probabilities; adult over adult interactions did not deviate from expectation based on encounter probability (Table 5.3).

Table 5.2 Summary of results from group scans recording age-related aggressive displacements between individual Red Knots at incoming tide, displaying the direction of the displacement (adult or juvenile chasing individual of their own age-group, adult chasing juvenile, and vice versa), at two sites, X (a seagrass patch) and Y (a bare patch) (see Figure 5.1).

				Relative probability of aggressive displacement (%)			
Site	N_{obs}	N_{ind}	% juv.	ad. ↔ ad.	ad. → juv.	juv. → ad.	juv ↔ juv
X	56	1969	39	18.5	27.5	4.7	49.3
Y	36	774	69	6.5	32.3	5.9	55.3

Table 5.3 Comparison of observed and predicted frequencies of aggressive interactions in 92 group scans on Red Knots.

	p^2 ad. ↔ ad.	pq ad. → juv.	pq juv. → ad.	q^2 juv. ↔ juv.
Observed > Expected	11	22	8	26
Observed = Expected	1	0	0	13
Observed < Expected	7	2	0	2
P (sign test, two-tailed)	0.481	<0.001	0.008	<0.001

DISCUSSION

Several pieces of evidence support our prediction that differences in the use of dangerous nearshore bare habitat rather than safer offshore seagrass is caused by individual differences in foraging ability and competitive strength. The nearshore bare zone was mainly used by juveniles. Even around high tide, when high numbers of – predominantly adult – birds were barred from offshore mudflats, the high percentage of juveniles in nearshore flocks was not diluted by the presence of adults, neither on bare, nor on seagrass habitat (Fig. 5.5). In fact, on bare habitat the percentage of juveniles tended to increase the higher the tide, suggesting that either a number of juveniles used the bare nearshore zone for supplementary feeding when lower seagrass areas had become submerged, or part of the adults that feed in nearshore bare habitat have left earlier to the high tide roost. We suggest that with the incoming tide good foragers with high abdominal profiles leave to the high tide roost early. Their higher energy state and corresponding lower marginal value of energy lead to higher metabolic costs of predation (Brown & Kotler 2004). This results in a 'giving-up *distance*' (analogic to 'giving-up density', Brown 1988) dependent on body state. Note that the body state of the juvenile Red Knots in our study, rather than being a *cause* of habitat choice (Houston & McNamara 1999), in our view should be regarded a *consequence* of their inferior foraging proficiency which caused the habitat choice. It seems optimal for such juveniles to choose for such dangerous areas in which they can achieve highest intake rates (as these intake rates are still relatively low, these juveniles remain in a low energy state – Table 5.1).

Birds perceived nearshore habitat (0–40 m) as more dangerous, as witnessed by their vigilance behaviour (Fig. 5.3). But, as we have seen, distance to shore correlated with flock size. As flock size is known to affect vigilance patterns (Krause & Ruxton 2002, Caro 2005), we cannot ascribe the decreasing vigilance with distance to cover entirely to predator success rate. Still, the latter explanation fits the results of Cresswell *et al.* (2010), who observed that Sparrowhawk success rate declined

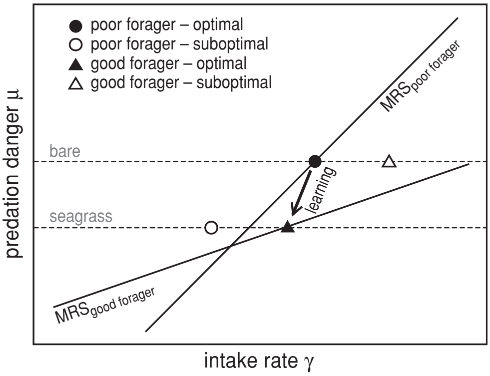


Figure 5.7 The available foraging options for poor and good foragers, illustrating when poor foragers, with age develop into good foragers, which should make a shift from one optimal foraging option to another.

exponentially with distance to predator-concealing cover; their threshold of approximately 30 m was very similar to the one of 40 m used here.

Our observations on agonistic interactions confirm that adults, compared with juveniles, are generally stronger competitors and better foragers who lose less time to aggressive interactions (Tables 5.2 and 5.3). The fact that juvenile birds were nearly six times more often displaced by adults than *vice versa* supports our prediction that subordinate juveniles suffer from interference competition by adult conspecifics. It also shows that differences in foraging skills alone cannot explain why age-classes segregate, and corroborate earlier studies reporting that adults are stronger competitors than juveniles (Goss-Custard & Durell 1987b, Cresswell 1994b, Minderman *et al.* 2006). An explanation for the high involvement of juveniles in agonistic interactions may lie in a lower proficiency in finding food causing juveniles to more often traverse the searching paths of other foragers. Such interference is expected to be highest when juveniles encounter other juveniles, which corresponds with the high frequency of mutual agonistic interactions among juveniles (2.7–8.5 times more often than among adults). In this way, competition and foraging skills may interact, such that less skilful foragers are more prone to interference with other foragers and more susceptible to aggression by dominants; otherwise, dominants may retard the learning process of inexperienced birds by competition (Goss-Custard & Durell 1987a, Caldow *et al.* 1999).

Consequently, poor foragers may gain higher intake rates by foraging in bare habitat at relatively large and easy retrievable bivalves (*Dosinia*) (Fig. 5.4) and with fewer competitors. Although as yet we were not able to test this within individuals, our field observations on energy intake rates in age-classes performing in either of the micro-habitats do support this idea: despite the lower available food densities in bare habitat, intake rates of juvenile foragers in this micro-habitat tend to be higher than in seagrass, while juveniles perform worse than adults in both micro-habitats (Table 5.1). Although the difference between intake rates of juveniles in bare and of (other) juveniles in seagrass was just not significant at the 5%-confidence level ($P = 0.097$), we have reasons to believe that the difference is biologically meaningful. The difference in juvenile intake rates in bare compared to seagrass habitat is still 20% larger than the significant difference – in the other direction! – between intake rates in bare vs. seagrass of all foragers taken together (Table 5.1). This indicates that we face not so much a lack of biological realism as of statistical power. Indeed, a power test revealed that 203 observations in each type of habitat would have been required to detect a statistically significant difference rather than the 158 and 35 intake-rate observations in bare and seagrass habitat, respectively, that we managed to collect. The second reason why we believe that the difference is biologically meaningful is that, as for the other comparisons, it concerns a difference between birds that *choose* to forage in either bare or seagrass habitat. In other words, as we compared intake rates *between* individuals instead of *within* individuals, the outcome of all comparisons are inevitably conservative, that is, differences would probably have been larger when testing within individuals.

Observations on colour-marked Red Knots in the same study site show that, with age, birds shift their foraging activities to safer patches (Chapter 6). This fits to a scenario in which poor foragers develop into good foragers, coinciding with a shift from one optimal foraging option to another (Fig. 5.7).

But why are abdominal profiles increasing in spring, at all distances from shore, including nearshore bare habitat? During this time adult Red Knots fuel up for migration. In case of food-safety trade-offs, their increasing energy requirements should lead them to accept more predation danger, because they experience higher marginal values of energy (Nonacs 1993, Houston & McNamara 1999, van Gils *et al.* 2005a). This is corroborated by the observed higher API's for each distance to cover (Fig. 5.6 C and D), and a reduced difference between near- and offshore API's (9.3% in spring vs. 51.5% in winter). When fuelling birds extend their working day they inevitably end up foraging closer to the dangerous shorelines. In addition, reduced overall predation danger may have contributed to a general tendency of birds with higher API's approaching the shorelines more. Raptor encounter probability in spring was lower (we speculate that this is caused by resident falcons leaving the area for breeding on offshore islands safe from jackals), which may have allowed foragers that formerly chose to forage further from cover to forage closer to shore, in places that used to be more dangerous. In any case, the fact that also heavier birds among juveniles, which generally do not prepare for migration, foraged closer to the shoreline in spring, suggests that 'marginal value of energy' is not an exclusive explanation. Thus, for birds that fuel up for migration probably the concerting effects of relaxed predation danger and higher marginal value of energy (Brown, 1999) make them decide to forage in nearshore foraging sites despite a reduced manoeuvrability due their higher fat loads (Cuthill & Houston 1997, Dietz *et al.* 2007).

Not only were differences in API between nearshore and offshore foragers smaller among juveniles in spring, juvenile API's in spring were also increased in general. This can be explained either by a number of juveniles having either died or recovered from a very low energy state (hence the abbreviation of the lower tail in the body mass range in catches from 84 to 99 g), or by a relaxed competition for food caused by the departure of adults to the breeding grounds that have allowed juveniles to increase their energy state.

It has been suggested that the non-lethal effects of predation on prey populations outweigh the mortality effects, and this suggestion has also been made for raptor-shorebird interactions (Cresswell 2008). Minor mortality effects of predation are often a reflection of highly effective, but costly, anti-predation measures taken by potential prey (Lima & Dill 1990, Lank & Ydenberg 2003). In our system, the anti-predation costs are the costs of feeding in a complexly structured seagrass habitat in which prey are abundant but harder to find and handle. Therefore, there is a high premium on developing foraging and competitive abilities which enables birds to feed in this much safer habitat, abilities that usually come with age.

BOX IV

Evaluating patch use decisions by extending Brown's patch use model with a parameter for interference

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Mary Ngozi Molokwu

One way of trying to understand why some birds forage in locations that are not only more dangerous but in which the danger is not compensated by higher food abundance, is by evaluating patch use decisions in the face of predation. We include the influence of stronger competitors by expanding the patch use model in Brown and Kotler (2004) with a parameter for competitive foraging. The patch use model is based on the patch departure rule, meaning that a forager should leave a patch at the point where energy gain no longer outweighs foraging costs (Brown, 1988). For our wintering Red Knots we assume that they attempt to maximize the probability of surviving over the non-breeding season with the requirement of maintaining a certain energy state. We therefore apply the following fitness formulation (Brown, 1988):

$$\text{Max } p \text{ subject to } F \geq k \qquad (1)$$

where p is the probability of surviving predation over a finite time interval. F is the survivor's fitness, and k is the individual's energy state.

For this fitness formulation Brown derived the optimal patch use strategy, stating that a patch should be left when the benefits of the reward rate H no longer exceeds the sum of metabolic costs C, predation costs P, and missed opportunity costs MOC of foraging. The MOC, which like the other costs may have units of energy per unit time, items per unit times, or units of resource per unit time, places a value on alternative fitness enhancing activities (Brown and Kotler, 2004). $H = C + P + MOC$, as derived by Brown for optimal patch strategy (Brown, 1992), can be recognized in the following formula:

$$H = C + \frac{\mu p}{\varphi_F\,(\delta_F/\delta_e)} + \frac{\varphi_t}{\varphi_F\,(\delta_F/\delta_e)} \tag{2}$$

Here μ is predation danger; it is converted into the currency of H by multiplying the predation danger by the marginal rate of substitution of energy for safety. δ_F/δ_e is de marginal value of energy. φ_t is the marginal fitness value of time if the time constraints were relaxed by providing more time, and φ_F is the marginal survivorship value of favourably adjusting the energetic-state constraint (Brown and Kotler, 2004, Olsson *et al.*, 2008).

We now extend equation 2 with the interference effects exerted by dominants, in this case adults N_a, and affecting the foraging costs experienced by subordinate juvenile birds. The dominants may influence the foraging costs of subordinates in several ways. First, we assume dominants to increase the metabolic cost of foraging C such that

$$C = c + \frac{a_m N_a}{X_m + N_a} \tag{3}$$

Here c denotes baseline metabolic foraging costs, a_m is the maximum adult effect, and X_m is the half-saturation constant.

Second, we assume that, within a patch, adults increase predation danger for juveniles, e.g. by chasing them towards intrinsically more dangerous foraging locations, such as the periphery of the group. We again assume a saturating effect, such that

$$\mu_j = m + \frac{a_p N_a}{X_p + N_a} \tag{4}$$

Here m is the baseline predation danger, a_p is the maximum adult effect, and X_p is the half-saturation constant.

Third, we assume adults to directly affect the feeding rate H such that the feeding rate becomes

$$H = f_j e^{-a_f N_a} \tag{5}$$

Here, f_j is the maximum feeding rate of a juvenile, which is slowed down by the presence of adults according to $e^{-a_f N_a}$, where a_f is a constant. Bringing these parts together and substituting in equation 2 gives:

$$f_j = c e^{-a_f N_a} + \frac{a_m N_a e^{a_f N_a}}{X_m + N_a} + p e^{-a_f N_a} \left(m + \frac{a_p N_a}{X_p + N_a} \right) + \frac{\varphi_t e^{a_f N_a}}{\varphi_f\,(\delta_F/\delta_e)} \tag{6}$$

The more additional foraging costs adults inflict upon a juvenile j, the fewer adults the latter should tolerate in its presence. In fact, the number of adults tolerated before the bird should leave the patch is determined by a foraging cost plateau set by the juveniles (Fig. IV.1). We evaluate the effects of predation on the number of adults tolerated by juveniles, by imposing three levels of predation costs related to

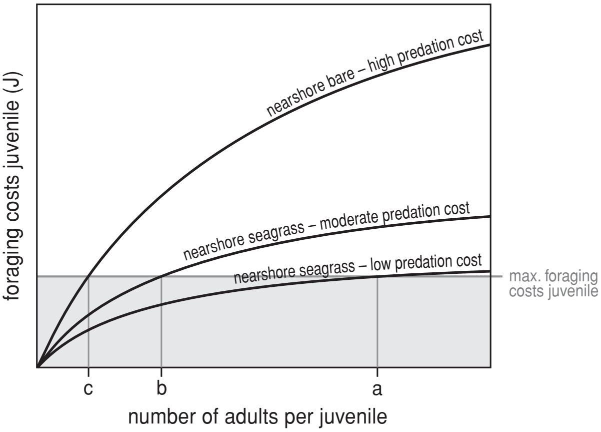
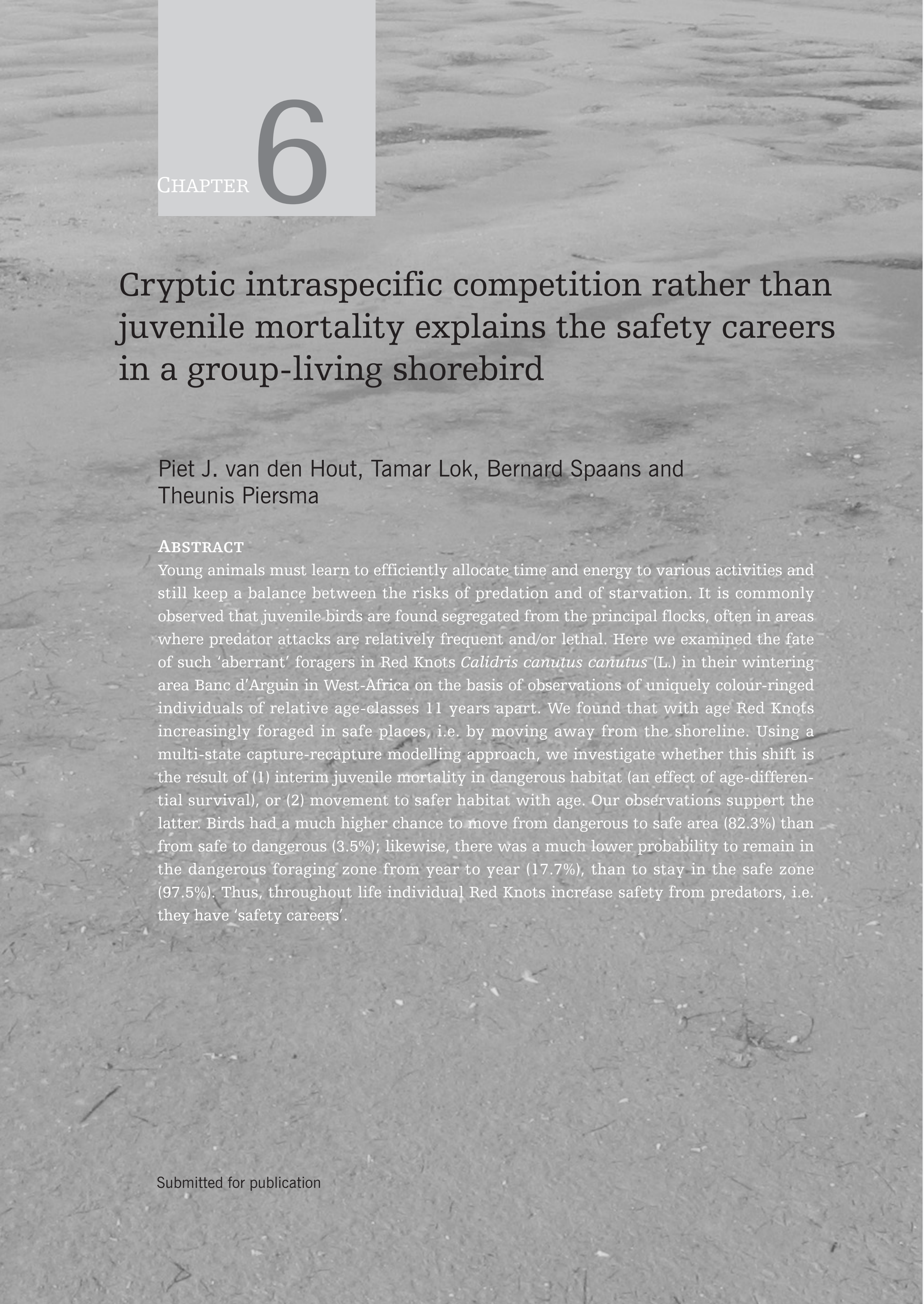


Figure IV.1 This graph shows the foraging costs as a function of the number of adults (dominants) relative to juveniles (subordinates) for three levels of predation costs, corresponding to far-shore seagrass (low cost), nearshore seagrass (moderate cost) and nearshore bare habitat (high cost). If foraging in a far-shore seagrass habitat, juveniles should leave when the foraging costs inflicted by adults cross the foraging cost plateau set by the juveniles and are forced to forage in a patch that incurs higher predation costs (from a to b). When incoming tide forces more adults to forage in near-shore seagrass they again drive juveniles towards a cost plateau forcing them to leave to near-shore bare habitat (from b to c).

habitat (near-shore bare, near-shore seagrass, and far-shore seagrass respectively; Fig. IV.1). Far-shore seagrass beds are safest as predators rarely hunt here (encounter probability of 0.03 raptors h^{-1}) and due to the openness of the landscape detection chances are high, so lethality of attack must be low. Seagrass beds at moderate distance to shore are more dangerous (encounter probability of 0.28 raptors h^{-1};), while the dune-bordered bare habitat are most dangerous for not only the encounter probability is relatively high (0.17 raptors h^{-1}), but as birds forage approximately 0-40 m from obstructive cover created by vegetated dunes, lethality of attack must be very high (Dekker and Ydenberg, 2004, van den Hout *et al.*, 2008, Cresswell *et al.*, 2010). Thus, we assign far-shore seagrass beds as ‘safe’, near-shore seagrass beds as of ‘moderately dangerous’, and near-shore bare habitat as ‘very dangerous’.

We predict that in a scenario where predation danger is not compensated by food abundance: (a) foraging decisions of subordinate birds must be governed by the foraging costs that dominant birds inflict of them, (b) in order to avoid starvation juveniles put a maximum on the foraging costs they accept, and (c) foraging cost levels increase as a function of danger, decreasing the threshold level of dominants that renders a patch unprofitable for a juvenile; the proportion of juveniles in a flock should therefore decrease with increasing numbers of adults at incoming and outgoing tides (Fig. IV.1, from a to b to c).

Although we have indications that such mechanisms actually occur (Chapter 5), we need more data on age-related foraging patterns, particularly in far-shore seagrass, to prove our point.



CHAPTER 6

Cryptic intraspecific competition rather than juvenile mortality explains the safety careers in a group-living shorebird

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Theunis Piersma

ABSTRACT

Young animals must learn to efficiently allocate time and energy to various activities and still keep a balance between the risks of predation and of starvation. It is commonly observed that juvenile birds are found segregated from the principal flocks, often in areas where predator attacks are relatively frequent and/or lethal. Here we examined the fate of such 'aberrant' foragers in Red Knots *Calidris canutus canutus* (L.) in their wintering area Banc d'Arguin in West-Africa on the basis of observations of uniquely colour-ringed individuals of relative age-classes 11 years apart. We found that with age Red Knots increasingly foraged in safe places, i.e. by moving away from the shoreline. Using a multi-state capture-recapture modelling approach, we investigate whether this shift is the result of (1) interim juvenile mortality in dangerous habitat (an effect of age-differential survival), or (2) movement to safer habitat with age. Our observations support the latter. Birds had a much higher chance to move from dangerous to safe area (82.3%) than from safe to dangerous (3.5%); likewise, there was a much lower probability to remain in the dangerous foraging zone from year to year (17.7%), than to stay in the safe zone (97.5%). Thus, throughout life individual Red Knots increase safety from predators, i.e. they have 'safety careers'.

Submitted for publication

INTRODUCTION

Most animals die relatively young (Lack 1954), and it may be argued that this 'juvenile mortality' relates to a kind of behavioural 'immaturity' or 'inability'. In addition, the shorter time that natural selection has had to weed out less well-adapted phenotypes, explains why the 'inept' individuals are most often juvenile (Rappole 1995). For instance, juveniles must acquire skills in predator avoidance (Caro 2005), foraging (Groves 1978; Burger 1980; Espin *et al.* 1983; Goss-Custard & Durell 1987a), and social interaction (Burger 1980), particularly with conspecific competitors (Goss-Custard & Durell 1987b; Wunderle 1991). Furthermore, juveniles must learn to efficiently allocate time and energy to these activities, so as to balance conflicting demands to reduce their vulnerability to both predation and starvation (Wunderle 1991).

Similarly, lower foraging proficiency and competitive ability may explain why juvenile birds are often found segregated from the principal flocks to forage in places where predator attacks are particularly frequent and/or lethal (van der Have *et al.* 1984; Ekman 1987; Goss-Custard & Durell 1987a; Cresswell 1994b). Should such foragers be considered a 'doomed surplus' (Errington 1946b), their lives soon being terminated either in the claws of a predator or by starvation? Or do these foragers in the course of life work their way up to safer foraging sites? If the latter would be the case, how long does it take for young birds to be as skilful and competitive as the experienced ones? What is needed are longitudinal studies of individuals, but so far these have been rare (but see Caldow *et al.* 1999).

He we document age-specific foraging distribution of uniquely colour-ringed Red Knots (*Calidris canutus*) in their main wintering area, the Banc d'Arguin, Mauritania. During the non-breeding season Red Knots are specialized molluscivores that prefer to feed on vast wide-open mudflats, generally in large flocks (Piersma 2007). On the Banc d'Arguin, the principal feeding grounds are offshore seagrass beds (Altenburg *et al.* 1982). These are the safest places to feed as these are rarely visited by falcons, the main predators of shorebirds. The falcons predominantly hunt in near-shore habitat, using low dunes to hide their approach and catch shorebirds by surprise (van den Hout *et al.* 2008). Yet, small flocks of primarily juvenile Red Knots forage in these near-shore areas (Van den Hout *et al.* submitted manuscript – Chapter 5).

In order to evaluate the age-related foraging distribution of Red Knots we contrast two alternative hypotheses to explain why older birds forage further away from the shoreline, i.e. in safer areas. These hypotheses involve two demographic processes: (1) survival and (2) movement. (1) Birds may make a single choice when they first arrive on their wintering destination and remain faithful to this foraging area throughout their lives (see Leyrer *et al.* 2006). Birds foraging close to the shore have lower survival due to predation than birds foraging further away. Areas that become available due to the death of individuals will become occupied by new juveniles and this will lead to a lower average age of individuals foraging in near-shore sites. (2) In case of 'movement', juveniles may initially choose to forage in sites where the density of conspecifics is relatively low and/or where they can achieve highest energy intake rates. In this case, their acceptance of high predation risk may either be the result of a trade-off between energy and safety (they feed in areas with low competition to compensate for their subordinate state and/or where food is easier to find), or caused by a biased assessment of the attractiveness of these near-shore sites due to their inexperience with the actual predation danger. With age, individuals gain more experience in foraging and may increase in dominance which thus enables them to shift to safer offshore foraging areas. Obviously, the observed distribution of age classes over the foraging area can also result from a combination of differences in survival and movement probability.

Here we use modern demographic modelling techniques to assess the relative roles of survival and movement in explaining the observed relationship between age and distance of foraging sites to obstructive cover along the shore. We frame the following – mutually non-exclusive – predictions: (1) Survival is higher in safe foraging areas compared to dangerous areas; (2) The probability to move from dangerous to safe area is higher than the probability to move from safe to dangerous and (3) Assuming that dominance rank and/or experience increases with age, we may expect that the probability of moving from dangerous to safe area increases with age.

METHODS

Study area

The Banc d'Arguin is an area of shallow water and islands that stretches along the northern coast of Mauritania, bordering the Sahara desert from about 20°50'N, 16° 45'W to 19°20'N, 16°28'W. Part of this area, including 500 km^2 of intertidal flats, is protected as a national park (Altenburg *et al.* 1982; Wolff & Smit 1990; Isenmann 2006). The fieldwork was carried out on and around the Iwik Peninsula (19°53'N, 16°17'W, Fig. 6.1). Of a total area of 50 km^2, approximately 22 km^2 is occupied by tidal mudflats which are largely covered by seagrass (*Zostera noltii*). Part of the mudflats is surrounded by vast expanses of sebkha (salt plains), partly bordered by low dunes (sites 1 and 2), which are used by falcons as cover for surprise attacks. The central part of the peninsula consists of low barren hills (not higher than around 15 m), which are favoured by large falcons (Lanner *Falco biarmicus*, Barbary *Falco peregrinoides* and Peregrine Falcon *Falco peregrinus*) as perching sites and points of departure for attacks. Some seagrass beds (sites 8 and 9, Fig. 6.1) are separated from the peninsula across the entire tidal cycle by an approximately 1–1.5 km wide channel. Other sites, including 6, 7 and 11, are separated from the mainland by narrow channels up to a few hundred meters. Site 6 harbours a narrow elongated ridge of approximately half a meter height, and an observation tower, which was commonly used as a perching place by one or two falcons throughout the winter.

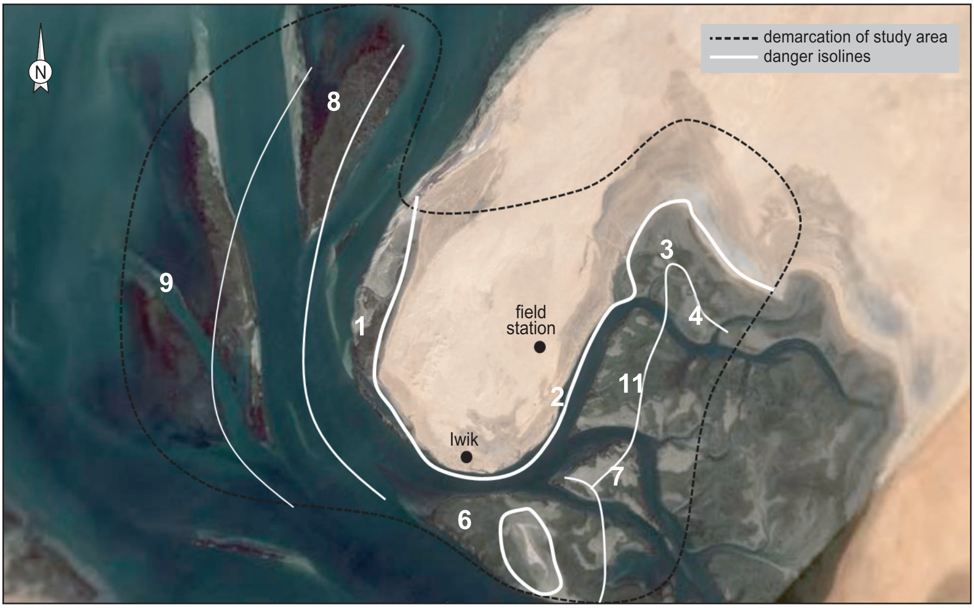

Figure 6.1 Study area, with isolines of distances to closest raptor-concealing cover (straight lines depart from the peninsula; dashed lines depart from an island (site 6) where a small dune ridge provides falcons with opportunities for both resting and surprise attack. As lines get thicker (closer to cover), danger is higher. Dark dashed lines represent the boundary of the study area.

The dune ridge was utilized by falcons as cover for surprise attacks, while the observation tower created an additional point of departure for attack.

Fiel methods

Each year we trapped shorebirds with mist-nets during the calm nights around the New Moon with the highest water levels (Piersma & Spaans 2004). Red Knots were assigned to age-class (1st winter, 2nd winter or older than 2nd winter bird) and marked with unique combinations of colour-rings (Leyrer *et al.* 2006; van den Hout *et al.* 2008). The age-class of an individual was based on true age, not calendar year. In Red Knots the ages of birds older than 2nd winter cannot be distinguished (Prater *et al.* 1977). This means that for individuals assigned to be older than 2nd winter at ringing their age in subsequent years must be considered relative.

Visual observations on colour-banded individuals were made by 42 observers in the months of November and December during the years 2004 to 2009. Observations of 11 adult (3 years or older) and 13 first-year Red Knots radio-tagged (and colour-ringed) in December 2006 were included in the analysis. Summaries are provided of the numbers of observation sessions (Table 6.1A) and the number of different individuals observed at each site (Table 6.1B). A detailed study in Scotland suggested that colour-ringing does not affect predation mortality (Cresswell 2007)."

Assessing levels of predation danger

Following Lank & Ydenberg (2003), we like to emphasize the difference between 'danger' and 'risk'. Predation risk, the probability of being depredated, is under some degree of control by an animal, whereas predation danger, an attribute of the environment, is not. Several studies on birds from open habitats have identified that proximity to obstructive cover is a major determinant of predation danger (Cresswell 1994b; Ydenberg *et al.* 2002; Dekker & Ydenberg 2004; Pomeroy 2006; van den Hout *et al.* 2008; Cresswell *et al.* 2010). In the study area, Red Knots confirm this assessment by showing higher levels of vigilance closer to shore (Van den Hout *et al.* unpubl. data - see Chapter 5). In the context of this paper, when

Table 6.1 Number of observation sessions per year and median distance from cover (A) and different birds observed per year (B) for the different study sites (upper table section, see Fig. 6.1) and per danger status (lower table section).

A Site	2004	2005	2006	2007	2008	2009	Distance to cover	Danger status
2	6	14	35	19	10	8	20	D
3	8	6	25	5	14	9	150	S
4	0	2	2	0	1	3	600	S
6	4	5	21	1	4	8	400	S
7	1	0	7	0	4	5	900	S
8	4	2	4	1	7	7	1200	S
9	5	7	23	2	4	4	1700	S
10	0	1	10	0	7	8	800	S
11	0	5	21	2	11	15	500	S
D	6	14	35	19	10	8		
S	22	28	113	11	52	59		

B Site	2004	2005	2006	2007	2008	2009
2	5	9	21	25	26	60
3	31	29	89	12	58	74
4	0	3	2	0	3	7
6	4	5	10	6	19	16
7	4	0	13	0	9	11
8	36	16	13	14	92	128
9	35	38	104	11	13	21
10	0	1	24	0	31	59
11	0	17	29	9	29	87
D	5	9	21	25	26	60
S	110	109	284	52	254	403

talking about dangerous or safe sites, we refer to the predation danger at these sites, not the predation risk of individuals foraging at these sites.

Distances to cover were defined as the shortest distance to cover from the midpoint of a site, and are conveyed by isolines in Fig. 6.1. On the basis of observations that vigilance (the rate of head-ups) drops off a distance of approximately 40 m, this distance to obstructive cover of 40 m was thus used to delineate the 'dangerous near-shore area' from the 'safe off-shore area'. Note that our estimates closely matches the one of Cresswell *et al.* (2010) who observed that sparrowhawk *Accipiter nisus* success rate with distance to predator-concealing cover declined exponentially after ca. 30 m.

On the basis of a distance to cover of 40 m, site 2 is dangerous and all other sites are safe (Fig. 6.1). The state of danger of an individual in a given year was determined by first calculating the relative presence at each site by dividing the number of observation sessions a bird was observed at a certain site by the total number of observation sessions at that site. As there is only one dangerous site, this automatically gives the relative presence in the dangerous state. In contrast, to estimate the relative presence in the safe state, we took the average relative presence over all safe sites where the individual was seen at least once, as an indicator that this site was part of the home range of the individual. If a bird was only observed at the dangerous site in a particular year, its status was defined as "dangerous". Similarly, if a bird was only observed at safe sites, its state of danger was "safe". When a bird was observed at both safe and dangerous sites, its status was determined by selecting the state in which it had the highest relative presence.

Multi-state capture-recapture modelling approach

Multi-state capture-recapture modelling can be used to separate the estimation of survival within and movement between states (Brownie *et al.* 1993; Lebreton & Pradel 2002), while also estimating encounter probability, which in capture-recapture studies is generally less than 1 (in 'conventional' mixed models this would result in a considerable amount of nasty missing values). It has been widely used to estimate movement between geographical sites (Hestbeck *et al.* 1991), but is equally suitable to estimate transition probabilities between other kinds of states, such as behavioural or reproductive states (Nichols *et al.* 1994). In addition, the recently developed program *E-Surge* allows the estimation of initial state probabilities (Choquet *et al.* 2009). Using *E-Surge*, we estimate the probability to initially be in safe or dangerous state and survival in and movement between these two states.

A common problem with multi-state models is that the number of parameters can easily become large, particularly when all possible probabilities are allowed to vary over time. As we only have a fixed amount of data available, estimating many different parameters would lead to poor inference on any of the parameters. As we are primarily interested in testing several *a priori* hypotheses about differences in initial state, survival and movement probabilities in relation to the state of danger, we decided to exclude temporal variation in initial state, survival and movement.

Moreover, resighting effort at the different sites did not substantially differ between years, and therefore we also excluded temporal variability in resighting probability. We modelled resighting probability as a function of state, as we expect a much higher resighting probability in dangerous area, given its very small surface and easy accessibility (by foot, instead of by boat) compared to the majority of safe area.

Based on our *a priori* hypotheses, we defined a candidate model set of 24 models combining different parameterizations for the initial state, survival and movement probabilities (Table 6.2). In the most parameterized "umbrella" model, initial state probability was a function of age class (1st winter, 2nd winter and >2nd winter); survival probability a function of state; movement probability a function of state, with the movement from dangerous to safe area additionally being a function of age class (1st, 2nd and >2nd winter) and resighting probability a function of state: $\pi_{a3}\phi_{s+d}\psi_{s+d.a3}P_{s+d}$. Goodness-of-fit of the umbrella model was tested, using the median c-hat test in program MARK (White & Burnham 1999). A slight lack of fit (overdispersion) was estimated ($\hat{c} = 1.16 \pm 0.007$ S.E.). Model selection was based on Akaike's information criterion taking into account small sample sizes and adjusting for the estimated level of overdisperion (QAICc, see Akaike 1973; Burnham & Anderson 2002). We computed QAICc weights for each model; the weights of all models sum to 1 and represent the relative likelihood of each model, given the data and model set (Burnham and Anderson 2002). The likelihood of the different parameterizations of each parameter was assessed by comparing the cumulative model weights ($\sum w_i$) and evidence ratios between different parameterizations.

RESULTS

The percentage of birds observed in safe foraging area increased with their age and extends far beyond the transition from 1st to 2nd winter (Fig. 6.2). When testing whether this pattern was caused by survival (young individuals die and get replaced by a new generation of young individuals), or movement (with age inexperienced

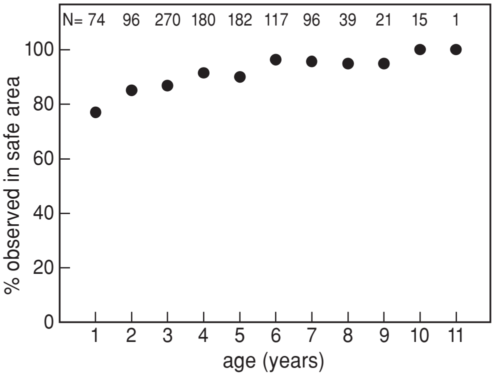

Figure 6.2 Percentage of individual Red Knots observed in the safe state as a function of (relative) age.

birds shift to safer foraging sites), we compared the models from the candidate model set (Table 6.2).

Models with constant survival ($\sum w_i = 0.731$) were 2.7 times more likely than the models with state variation in survival ($\sum w_j = 0.269$). Prediction 1 ("survival is higher in safe foraging areas compared to dangerous areas") is thus rejected, with survival being not significantly different for birds foraging in safe (offshore) versus dangerous (near-shore) areas. However, the confidence interval around the estimated survival probability in dangerous area is very large (0.45–0.95 in the highest ranked model with state variation in survival).

The probability to move from dangerous to safe area was much higher than the probability to move from safe to dangerous area (see Table 6.3). Complementary to this, the probability to stay in dangerous area was much lower than to stay in safe area. This result was highly significant as indicated by the models with state variation in movement probability ($\sum w_i = 0.998$) being 535 times more likely than models

Table 6.2 List of *a priori* models. Each combination of parameterizations is tested, resulting in 24 models.

Parameterizations	Description
Initial state (π)	
.	no age differences in probability to be in either state
a2	the probability to be in either state differs between 1st winter and older birds
a3	the probability to be in either state differs between 1st winter, 2nd winter and older birds
Survival (ϕ)	
.	survival does not differ between states or age classes
d+s	survival differs between birds in dangerous versus safe state
Movement (ψ)	
.	probability to move from dangerous to safe state is the same as the probability to move from safe to dangerous state (complementary to this: probability to stay in dangerous state is the same as the probability to stay in safe state)
d+s	probability to move from dangerous to safe state is different than to move from safe to dangerous state
d.a2+s	probability to move from dangerous to safe state differs between 1st winter and older birds; probability to move from safe to dangerous state does not depend on age
d.a3+s	probability to move from dangerous to safe state differs between 1st winter, 2nd winter and older birds; probability to move from safe to dangerous state does not depend on age
Resighting (p)	
d+s	Probability of resighting is different for birds in dangerous versus safe state

without state variation ($\sum w_i = 0.002$). We thus found strong evidence for Prediction 2 ("the probability to move from dangerous to safe area is higher than the probability to move from safe to dangerous").

The models with age variation in the probability to move from dangerous to safe area ($\sum w_i = 0.891$) were 8.3 times more likely than models without age variation ($\sum w_i = 0.107$). The models with two age classes (1^{st} year versus older birds) ($\sum w_i = 0.627$) were slightly more likely (2.4 times) than models with three age classes (1^{st} year versus 2^{nd} year versus older birds) ($\sum w_i = 0.264$). In the model with two age classes, the probability to move from dangerous to safe area was significantly lower for the transition between 1st and 2nd winter (56%), than for later transitions (92%; Tables 6.3 and 6.4). Prediction 3 ("the probability of moving from dangerous to safe area increases with age") is therefore accepted, although the exact magnitude of age differences in movement probabilities remains uncertain.

Table 6.3 Best models (with QAICc-weight ≥ 0.01) from the candidate model set (see Table 6.2).

Model	# Par	Deviance	QAICc	QAICc-weight
π_{a2} $\phi_{.}$ $\psi_{s+d.a2}$	8	2150.75	1870.23	0.33
π_{a2} $\phi_{.}$ $\psi_{s+d.a3}$	9	2150.40	1871.96	0.14
π_{a3} f. $\psi_{s+d.a2}$	9	2150.67	1872.19	0.13
π_{a2} ϕ_{d+s} $\psi_{s+d.a2}$	9	2150.71	1872.23	0.12
π_{a2} $\phi_{.}$ ψ_{s+d}	7	2157.20	1873.76	0.06
π_{a3} $\phi_{.}$ $\psi_{s+d.a3}$	10	2150.31	1873.92	0.05
π_{a2} ϕ_{d+s} $\psi_{s+d.a3}$	10	2150.36	1873.96	0.05
π_{a3} ϕ_{d+s} $\psi_{s+d.a2}$	10	2150.63	1874.19	0.05
π_{a3} $\phi_{.}$ ψ_{s+d}	8	2157.11	1875.71	0.02
π_{a2} ϕ_{d+s} ψ_{s+d}	8	2157.19	1875.78	0.02
π_{a3} ϕ_{d+s} $\psi_{s+d.a3}$	11	2150.27	1875.93	0.02
π_{a3} ϕ_{d+s} ψ_{s+d}	9	2157.10	1877.74	0.01

Table 6.4 Parameter estimates of the best model ($\pi_{a2}\phi_{.}\psi_{s+d.a2}$).

Parameter	Estimate	CI-	CI+	SE
$\pi_{1^{st}\text{ winter, safe}}$	0.77	0.65	0.86	0.05
$\pi_{\text{older, safe}}$	0.92	0.90	0.94	0.01
$\phi_{.}$	0.77	0.71	0.83	0.03
$\psi_{\text{d-s, }1^{st}\rightarrow 2^{nd}\text{ winter}}$	0.56	0.25	0.83	0.17
$\psi_{\text{d-s, Age}\rightarrow\text{Age}+1\text{, where Age}\geq 2^{nd}\text{ winter}}$	0.92	0.75	0.98	0.05
$\psi_{\text{s-d}}$	0.04	0.02	0.05	0.01
p_{safe}	0.28	0.24	0.34	0.03
$p_{\text{dangerous}}$	1.00	1.00	1.00	0.00

DISCUSSION

This study shows that the dangerous near-shore habitat does not necessary represent an ecological sink for Red Knots. The observed distribution, with more birds, and more adult birds in particular, foraging in safe area, was explained by a difference in movement probability, that is, a higher probability to move from dangerous to safe habitat than vice versa, and not by a difference in survival. This probability was lower in juveniles than in older birds. This reveals that the age-distribution we observed is not merely a result from higher interim mortality of (primarily young) individuals in dangerous habitat.

We could not detect a difference in mortality between birds in dangerous and in safe state. This could be due to the low sample size in the dangerous zones, which were used by only 24.3 ± 7.9 (avg ± SE; range 5-60) colour-ringed birds across the years (compared to 202 ± 54.6 (avg ± SE; range 52-503) birds in safe area; Table 6.1B). Yet, van den Hout *et al.* (2008) report low mortality rates at Banc d'Arguin (only 1% of the juveniles in this population were killed over a winter), which suggests that, rather than in direct mortality, the effects predation danger were reflected in anti-predation behaviours, such as vigilance (P. J. van den Hout, J. A. van Gils, F. Robin & T. Piersma, unpublished data - see Chapter 5).

Patterns of age-related distribution have been reported to be the result of differences in foraging skills (Caldow *et al.* 1999) or in competitive ability (Fretwell & Lucas 1970; Cresswell 1994b; Bautista *et al.* 1995; Minderman *et al.* 2006), often in combination (Caldow *et al.* 1999). In our case both mechanisms may have contributed to the age patterns. In a related study, juvenile birds were found to be more often displaced by aggression by older birds than vice versa (Van den Hout *et al.* submitted manuscript – Chapter 5). So, competitive exclusion may have contributed to the observed age-related pattern in habitat use. Yet, in the same study area birds were observed to use bare near-shore habitat (< 40 m from shore), which is poorer in food than near-shore seagrass beds at times when the richer near-shore seagrass beds are available and visited by few competitors. This indicates that competitive exclusion from seagrass beds cannot fully account for near-shore foraging, while foraging skills may contribute to this choice of habitat (Van den Hout *et al.* submitted manuscript – Chapter 5).

Among shorebirds, Oystercatchers *Haematopus ostralegus* are one of the few species in which the ontogeny of foraging and related habitat use was studied on the individual level, revealing that through competition adults may retard the rate at which juveniles learn foraging on mussel beds on the most profitable prey types (Goss-Custard & Durell, 1987a,b). We now add another example in a flock-living shorebird species, showing that changing patterns of habitat use with age may in fact be the result of increasing proficiencies of individuals and not just a matter of interim mortality of incapable foragers.

Most shorebird studies consider a learning curve in foraging skills and competitiveness that strongly levels off after the juvenile stage in life, and compare adults with juveniles in studies concerned with habitat use (Kus *et al.* 1984; van der Have *et al.* 1984; Wunderle 1991; Cresswell 1994b, but see Caldow *et al.* 1999). Our study indeed shows a strong transition from dangerous to safe habitat, particularly after the first year. Yet, after a transition of 56% of the juveniles to safer habitat in their 2nd winter, still 44% remain in safe habitat, whereas a larger shift to safer habitat occurs after the 2nd winter (Table 6.3).This suggests that for a number of birds it takes more years to acquire fully matured skills. In fact, delayed breeding by Red Knots to at least three or four years of age (Piersma *et al.* 1996) may not only be constrained by sexual maturity but also by the high standards required to develop their highly specialised foraging techniques (Piersma *et al.* 1998; Durell 2000); van den Hout *et al.* submitted manuscript - Chapter 5), which should enable them to survive winter and migration, and allow them to breed within the narrow constraints of the arctic summer. In any case, competition for safety seems to be a life-long issue for Red Knots.

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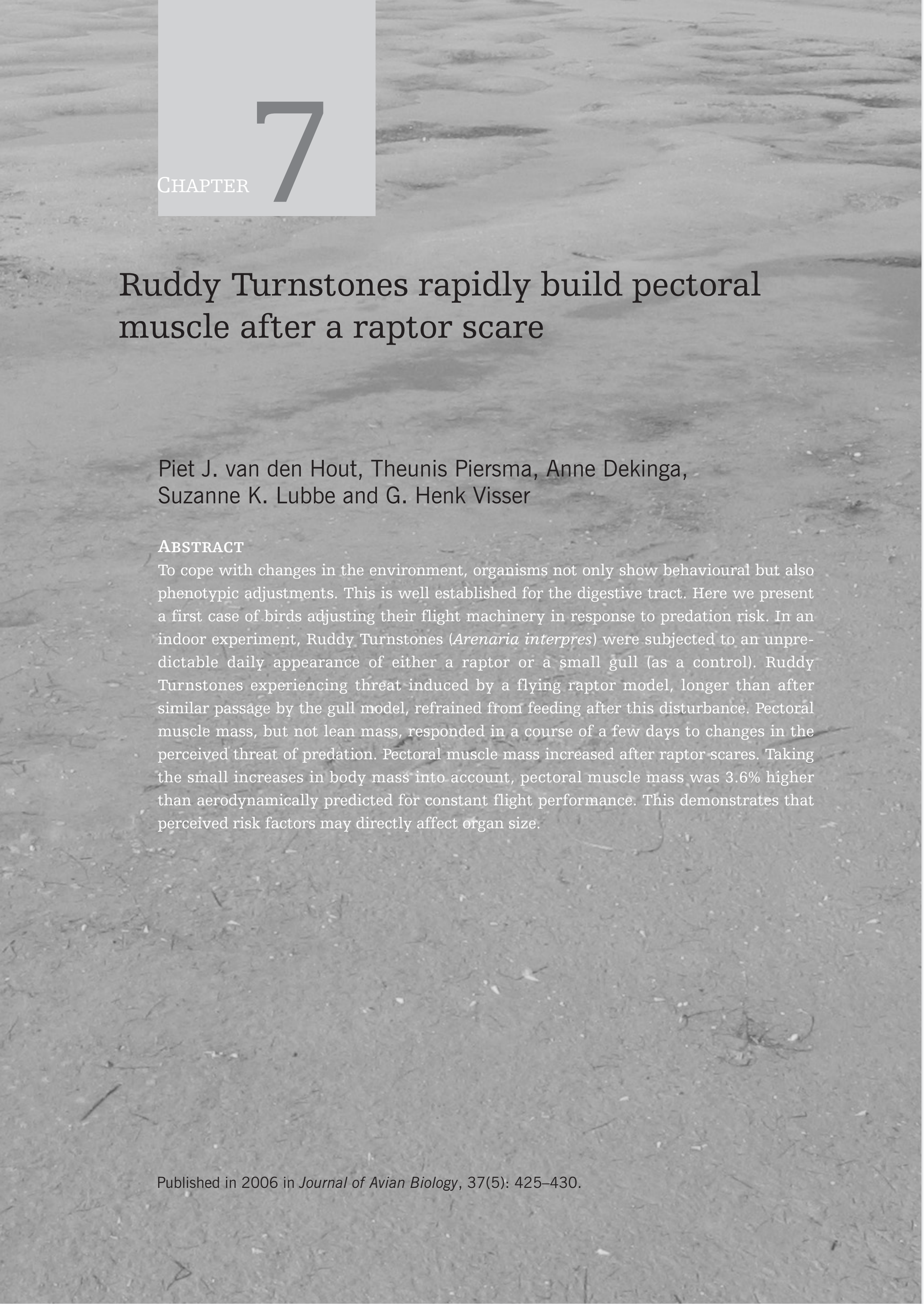
PART III

ADAPTIVE FLEXIBLE PHENOTYPIC RESPONSES TO PREDATION DANGER



Chapter 7

Ruddy Turnstones rapidly build pectoral muscle after a raptor scare

Piet J. van den Hout, Theunis Piersma, Anne Dekinga,
Suzanne K. Lubbe and G. Henk Visser

Abstract

To cope with changes in the environment, organisms not only show behavioural but also phenotypic adjustments. This is well established for the digestive tract. Here we present a first case of birds adjusting their flight machinery in response to predation risk. In an indoor experiment, Ruddy Turnstones (*Arenaria interpres*) were subjected to an unpredictable daily appearance of either a raptor or a small gull (as a control). Ruddy Turnstones experiencing threat induced by a flying raptor model, longer than after similar passage by the gull model, refrained from feeding after this disturbance. Pectoral muscle mass, but not lean mass, responded in a course of a few days to changes in the perceived threat of predation. Pectoral muscle mass increased after raptor scares. Taking the small increases in body mass into account, pectoral muscle mass was 3.6% higher than aerodynamically predicted for constant flight performance. This demonstrates that perceived risk factors may directly affect organ size.

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INTRODUCTION

It is becoming evident that evolutionary design processes that affect behaviour (general activity, habitat use, daily routines), also affect physiological processes, including the size of functional organs, and that they do so over similar time scales (Piersma and Drent 2003). In every organism where it has been studied, the digestive tract responds rapidly and in highly integrated ways to variations in food quality and energy demand (e.g. Van Gils *et al.* 2003, Van Gils *et al.* 2005a, Starck & Rahmaan 2003, Starck 2005, Pennisi 2005). Free-living organisms are affected in major ways by the danger of predation (Lima & Dill 1990, Cresswell 1994a, Caro 2005). For example, incorporating risk management into the suite of selective pressures, Relyea & Auld (2004) found that tadpoles of the Wood Frog (*Rana sylvatica*) that grew up in pools with predators showed slower growth because they invested in tails (for swimming speed) rather than guts (for food processing).

Building on the knowledge that the main flight organ of birds, the pectoral muscle complex, demonstrates size variability in a seasonal context (Marsh 1984; Evans *et al.* 1992, Jehl 1997, Piersma *et al.* 1999), Lind (2001) suggested that moulting Tree Sparrows (*Passer montanus*) increased pectoral muscle size to reduce risk of predation by airborne raptors (see also Lind & Jakobsson 2001). Here we demonstrate that a perceived threat of predation may directly affect organ size, by showing that Ruddy Turnstones (*Arenaria interpres*), exposed to one sudden disturbance per day of a model of a dangerous raptor rather than an innocuous small gull, increased pectoral muscle size.

METHODS

Ruddy Turnstones are medium-sized shorebirds that feed on small prey in nearshore habitats in small flocks, where the risk of predation by surprise-attacks may be relatively high (Metcalfe & Furness 1984, Whitfield 1990). Thirty birds were captured on a high tide roost in the Wadden Sea, The Netherlands, in November 2002. They were kept in two separate flocks of 15 birds in indoor aviaries at the Royal Netherlands Institute for Sea Research (NIOZ).

The experiments took place from March to June 2003 in an 8 × 7 m wide and 3 m high indoor aviary in which a mudflat system was created. Three food trays supplying *ad libitum* food (Trouvit fishmeal pellets, Trouw Nutrition, The Netherlands) were placed evenly across the mudflat. A roosting area of 2 × 1 m was constructed in a corner of the mudflat. A constant light and tidal regime were implemented, with high tides in darkness (‘moonlight’ illumination available; food trays on high tide roost) between 1800 and 800 h.

For general habituation all birds were kept in the experimental aviary for a week. Thereafter birds were kept in the two smaller aviaries of 3.85 × 1.85 × 2.40 m, and five birds were randomly selected for each experiment. After the experiments the birds were moved to outdoor aviaries where they were kept until release as one flock in June 2003.

Not to face the concern that our experiment tested for effects of disturbance rather than the threat of a raptor per se, we chose to use a gliding raptor model against a model of an innocuous gull. A threat of predation was induced by gliding the raptor along a line along one wall of the aviary, once a day but at unpredictable times between 0900 and 1700 h. Initially we used a Peregrine Falcon (*Falco peregrinus*) model. However, because turnstones seemed so extremely secure in the indoor enclosure, from the fourth trial onwards, we replaced the falcon by a Sparrowhawk (*Accipiter nisus*), a species known to catch shorebirds on the ground (Cresswell 1996), and, from the third trial onwards, played shorebird alarm calls recorded at a roost as the 'predator' approached . The control treatment throughout consisted of passage by a stuffed Black-headed Gull (*Larus ridibundus*), with gull contact calls played from the fourth trial onwards.

We carried out six trials, each consisting of two treatment periods. Four trials started with the control disturbance and two with the raptor disturbance. The first three trials lasted two weeks, with treatment periods of seven days. After three trials we concluded that we missed time for habituation to the new environment. In order to keep the overall experimental duration constant, we subsequently used the first week for habituation. This necessarily restricted the treatment periods to 3.5 days each. All variations in experimental procedures are presented in Table 7.1, the statistical effects of which were accounted for in the analysis (see Table 7.2).

During the experiments we kept a continuous record of the birds' activities. Upon appearance of the model intruder, the turnstones usually froze. As a behavioural measure of disturbance caused by the two types of models, we recorded, by direct observation, the time between the glide of the model and the moment that the birds resumed their normal activities, usually foraging (see Dill & Gillett 1991, Gotceitas & Godin 1991 for studies focussed on interrupted feeding).

Morphological changes were measured at the onset and at the end of each treatment period. Body mass was measured to the nearest 0.1 g on a Sartorius balance, type 3862. Pectoral muscle size (muscle thickness, to the nearest 0.1 mm) was measured by AD using a Pie 200 ultrasound apparatus with a 7.5 MHz linear probe (Pie Medical Benelux BV, Maastricht, The Netherlands; for further details, see Dietz *et al.* 1999a). To prevent observational bias, these measurements were performed without knowledge of either the history of the measured individual or the outcomes of the measurements (double-blind). These experiments showed a repeatability of 0.83 (Dietz *et al.* 1999a). We computed pectoral muscle mass (PMM) (g) from muscle thickness (MT) (mm) using the predictive equation derived from a calibration exercise on similarly dimensioned Red Knots (*Calidris canutus*): PMM = $-10.93 + 31.73 \times$ MT ($r^2 = 0.797$, $P < 0.001$; Dietz *et al.* 1999a) (note that the absolute mass estimate is not important, but the relative mass change is). During the last experiment no pectoral muscle data were obtained because of instrument failure. We thus limited the comparisons involving body mass components to the first five trials.

To estimate lean (fat-free) mass (and, by subtraction from body mass, the fat mass), at the start, after control and after raptor treatments, we determined the size of the body water pool by stable isotope dilution. Procedures are presented in detail by Visser *et al.* (2000). Briefly, birds were injected subcutaneously above the pectoral muscle with 0.25 g isotope enriched water (^2H_2O). The exact amount injected was determined by weighing the syringe (in g) to the fourth decimal before and after the injection. To obtain background values of ^2H (deuterium), prior to this treatment blood samples were gathered from three birds (out of five). An hour after deuterium was injected, blood samples were taken for investigation of changes in the body water pool. All blood samples were taken by puncturing the brachial vein and collecting four samples of 15 μl of blood in micro-capillary tubes. The tubes were immediately sealed in a flame and stored by 4°C until analyses. All injections were made by AD.

Isotope enrichments of blood samples were determined in triplicate at the Centre for Isotope Research, University of Groningen, The Netherlands. Using an infrared mass spectrometer ^2H equilibration concentrations in the blood samples were determined (values were recalculated to ppm). Based on doses of ^2H injected, the ^2H dilution space was then calculated (in g) (Visser *et al.* 2000). As the ^2H dilution space is assumed to overestimate the actual amount of body water by 5%, calculations of total body water were corrected for this. Finally, lean wet mass (g) was determined assuming a constant water content of 69% (Piersma & Van Brederode 1990). For the first trial start values could not be obtained, which limited sample sizes for lean and fat mass to four trials (20 birds).

Using repeated measures, each individual served as its own control. To statistically control for the effects of treatment order (control or predator first) within an experiment, the individual experiment (named 'group') and the individual itself on the variables of interest (i.e. body mass, pectoral muscle size, lean mass and fat

Table 7.1 Overview of the experimental set-up.

Trial	No of birds	Habituation period	Experimental period (days)	Calls	Predator ID	Control ID	Predator or control first?	Successful pectoral muscle measure
1	3	0	14	-	Falcon	Gull	C	+
2	5	0	14	-	Falcon	Gull	P	+
3	5	0	14	+	Falcon	Gull	C	+
4	5	7	7	+	Hawk	Gull	P	+
5	5	7	7	+	Hawk	Gull	C	+
6	5	7	7	+	Hawk	Gull	P	-

The heterogeneity due to the length of habituation and trial period and presence of calls was statistically accounted for by examining the effect of trial number (see Methods and Table 7.2).

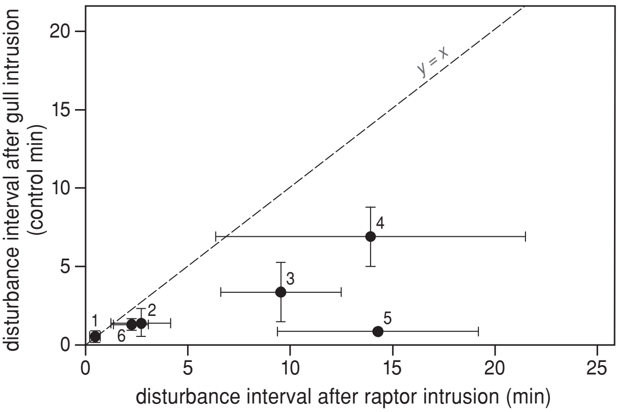

Figure 7.1 The time interval between the disturbance (by raptor or gull) and the resumption of activities. The *y*=*x* line helps to show that after raptor disturbance birds suspended their activities for the longest period. The numbers indicate the trials.

mass), we performed nested ANOVA using the GLM module in SYSTAT. Accordingly, to remove body size related variation among individual birds, all mass variables were standardised, by dividing them by the values at the start of the trial. Effects of the factor order were tested against the random factor group, effects of group were tested against the factor individual; all other terms were tested against the error term (Montgomery 2001). Post-encounter disturbance interval was measured on group level. Assumptions of normality and homoscedasticity were verified by visual inspection of probability plots. The mass values are presented as least square means ± se. Two birds drowned during the experiment, so one experimental group contained three rather than five birds (see Table 7.1).

RESULTS

Exposure to the avian models usually produced a behavioural response from the turnstones, which froze for some time, stayed put, or crouched down on their heels. The effect of a simulated raptor scare was significantly larger than of a more neutral (gull) scare: the disturbance intervals after exposure (i.e. the time interval between disturbance and restart of activities; Fig. 7.1) were much longer for the raptor treatment (7.3 ± 1.5 min) than for the control treatment (2.0 ± 1.4 min; $P = 0.014$; Table 7.2). In this case, and for all the phenotypic variables discussed next, the heterogeneity in the details of the experimental design did not affect the factors of interest (Table 7.2).

Body composition data indicate that while both bird models elicited some physiological responses in the turnstones, the raptor threat resulted in the largest and longest-term responses. This is evident in comparisons of trials where the order in

Table 7.2 GLM test results for effects on post-encounter disturbance interval, body mass, pectoral muscle size, lean mass, and fat mass. The factor of main interest, predation threat, and significant effects, are indicated in bold. Sum of squares of the phenotypic variables were multiplied by 100.

Source of variation	SS	df	F	*P*
BEHAVIOUR				
Dependent variable: post-encounter disturbance interval				
Order	21.9	1	0.3	0.641
Group(order)	245.6	3	2.3	0.091
PREDATION THREAT	232.9	1	6.6	**0.014**
Predation threat * order	41.9	1	1.2	0.282
Error	1192.1	34		
PHENOTYPIC VARIABLES				
Dependent variable: pectoral muscle size				
Order	5.3	1	1.7	0.321
Group(order)	9.4	2	4.1	**0.033**
Individual(group(order)	20.4	18	6.4	**<0.001**
Predation threat	2.4	1	13.5	**0.001**
Predation threat * order	0.9	1	4.9	**0.038**
Error	3.7	21		
Dependent variable: body mass				
Order	11.9	1	4.8	0.160
Group(order)	7.5	2	3.4	0.056
Individual(group(order)	19.8	18	13.7	**<0.001**
Predation threat	0.5	1	6.3	**0.020**
Predation threat * order	0.0	1	0.5	0.475
Error	1.7	21		
Dependent variable: lean mass				
Order	0.6	1	11.9	0.367
Group(order)	1.0	2	10.0	0.168
Individual(group(order)	3.8	15	5.0	**0.001**
Predation threat	0.1	1	1.1	0.312
Predation threat * order	0.0	1	0.7	0.424
Error	0.9	17		
Dependent variable: fat mass				
Order	38.2	1	4.2	0.177
Group(order)	18.1	2	0.8	0.469
Individual(group(order)	170.8	15	6.5	**<0.001**
Predation threat	1.6	1	0.9	0.346
Predation threat * order	1.8	1	1.0	0.330
Error	29.7	17		

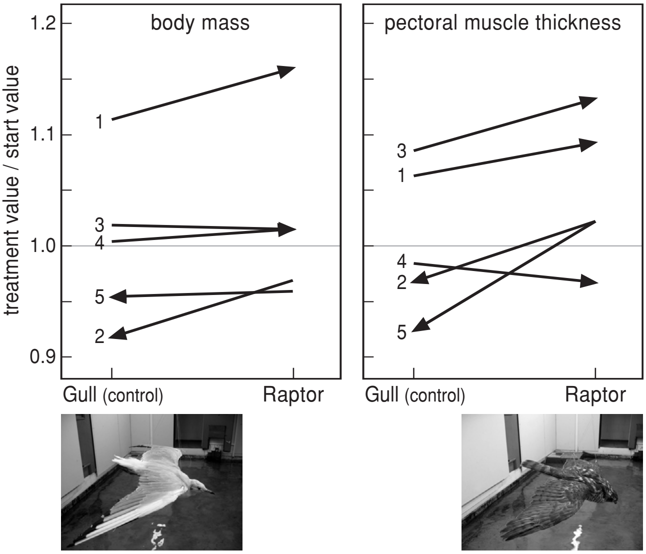

Figure 7.2 Changes in body mass (A) and pectoral muscle size (B) due to simulated raptor attack compared with control treatment (gull), shown for each of the trials separately (numbered by 1-5). The direction of each arrow reflects the treatment order (predator after gull or *vice versa*). The values were standardised to the values measured at the onset of the trial and are averages of five birds (except for the first trial: only three birds).

which the models were presented was reversed. When the raptor was presented first, pectoral muscle thickness increased by 3.8% from an average of 1.27 ± 0.01 cm to 1.32 ± 0.02 cm. When subsequently the same birds were exposed to the control model, pectoral muscle size dropped with 7.2% to 1.22 ± 0.02 cm. In contrast, while the gull-first treatment resulted in an initial increase in pectoral muscle size (to 1.35 ± 0.02 cm), exposure to the raptor model caused a further 1.8% increase in muscle size (to 1.37 ± 0.02 cm). This interaction between treatment and order was significant for the pectoral muscle (P=0.038), but was not found for body mass ($P = 0.475$; Table 7.2). Body mass decreased by 2.8% in the raptor-gull sequence (from 107.6 ± 1.0 g to 104.6 ± 1.0 g) and increased by 1.4% in the gull-raptor order (from 116.8 ± 0.89 g to 118.5 ± 0.89 g).

Overall, regardless of treatment order, exposure to the raptor model resulted in a change in body composition and mass. Average pectoral muscle thickness at the start of the experiment was 1.29 ± 0.02 cm. Birds that were exposed to the raptor model for 3–7 days increased pectoral muscle size by 4.1% while the same birds decreased pectoral muscle size by 0.5% during periods with a daily intrusion by the gull model (start = 1.29 ± 0.02 cm, raptor treatment = 1.34 ± 0.01 cm, control treatment = 1.28 ± 0.01 cm; $P = 0.001$; Table 7.2, Fig. 7.2).

Lean mass of the turnstones did not differ among treatments, being 82.6 ± 0.8 g at the start, 82.8 ± 2.3 g after the raptor scares, and 81.8 ± 2.3 g after the control disturbances (*P* = 0.312; Table 7.2). Fat mass, calculated by subtraction of estimated lean mass from body mass, was not affected by treatment either (27.4 ± 1.7 g at the start, 26.7 ± 0.8 g after the raptor encounters, and 25.6 ± 0.8 g after the control; *P* = 0.346; Table 7.2).

DISCUSSION

We found that captive Ruddy Turnstones were capable of distinguishing between the apparent threat of an avian predator and a similar-sized bird that posed no real threat. Behaviourally, turnstones showed a longer interruption to their regular routines when exposed to a raptor rather than a gull. Furthermore, disturbances by model birds elicited a response in the form of changes in the flight apparatus that were greater when birds were exposed to the threat of raptor predation.

When the 'innocuous' gull model was the first to be presented, turnstones initially increased pectoral muscle size. This indicates that in the context of a 'safe' indoor aviary, even a neutral object can be perceived as a risk. If so, then an increase in pectoral muscle size in birds exposed to the raptor model, and the subsequent decrease when exposed to the control model, could be interpreted as birds becoming accustomed to novel intrusions. However, when the reverse order of the model was presented - gull first followed by the raptor, the secondary response was a further increase in muscle mass, clearly indicating that turnstones were responding differentially to the control and predator treatments. Furthermore, regardless of the experimental order, raptor scares resulted in overall increases in pectoral muscle size and mass whereas the control treatment did not.

Although body mass and pectoral muscle size changed in the same direction after disturbances with a raptor (a Peregrine Falcon or a Sparrowhawk) rather than a control (gull), the change was more than twice as large in pectoral muscle. Apparently, in this context, pectoral muscle size was not a constant fraction of body mass as suggested by Biebach (1998), Piersma *et al.* (1999) and Lindström *et al.* (2000), but was effectively decoupled from it (Lind *et al.* 2001). This may reflect a strategic choice for an increase in escape capability (Lind *et al.* 2001; Kullberg, Jakobsson, Kaby *et al.* 2005).

Using Dietz *et al.* (1999a) (see methods), the overall difference in muscle thickness (start = 1.29 ± 0.02 cm, raptor treatment = 1.34 ± 0.01 cm, control treatment = 1.28 ± 0.01 cm) translates into pectoral muscle masses of 30.0 ± 0.65 g before the disturbances, 31.7 ± 0.27 g after the raptor scares and 29.8 ± 0.27 g after the gull intrusions (5.6% increase versus 0.6% decrease). Body mass increased by 1.4% in the raptor treatment, but decreased by 0.7% in the control treatment (start =111.5 ± 1.8 g, raptor model = 113.0 ± 0.67 g, gull model = 110.7 ± 0.67 g; *P* = 0.020; Table 7.2, Fig 7.2).

Subtraction of the estimated pectoral muscle mass values from the estimates of lean mass suggest that increases in pectoral muscle mass may have come at the expense of other lean tissue. Calculated pectoral-free lean mass changed from 52.6 g at the start of trials, to 50.7 g after raptor scares and 51.3 g after the control intrusions by the gull model.

Based on aerodynamic considerations, Dietz *et al.* (submitted MS) predicted that for flight performance to remain constant, pectoral muscle mass should allometrically scale with body mass to the power 1.25. With an average body mass of 110.7 g and a pectoral muscle of 29.8 g after the control treatment, for a constant flight performance turnstones (with an average body mass of 113.0 g) exposed to raptors are predicted to have a pectoral muscle mass of 30.6 g. The actual estimate of 31.7 g is 3.6% above this prediction. We thus suggest that turnstones exposed to raptors were prepared to boost flight performance by an additional investment in pectoral muscle size. At this point we remain ignorant about the causal factors translating fear into bigger muscles.

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CHAPTER 8

Differential responses of Red Knots, *Calidris canutus*, to perching and flying Sparrowhawk, *Accipiter nisus*, models

Kimberley J. Mathot, Piet J. van den Hout, and Theunis Piersma

ABSTRACT

According to the threat-sensitive predator avoidance hypothesis, prey should match the intensity of their anti-predation response to the degree of threat posed by predators. We used controlled indoor experiment to investigate the ability of Red Knots, *Calidris canutus*, to discern between high- and low-threat encounters with a representative predator, the Sparrowhawk, *Accipiter nisus*. The behaviour of knots was compared across three conditions: no predators present (very low predation threat), presentation of a perching Sparrowhawk model (low predation threat), and presentation of a gliding sparrowhawk model (high predation threat). In all behavioural parameters measured, Red Knots showed evidence of discriminating between the different levels of predation risk. Knots responded immediately to the presence of Sparrowhawks with escape flights, and the duration of escape flights was longer following the gliding Sparrowhawk events compared with perching events. Similarly, the proportion of time spent vigilant increased with increasing level of predation threat, while the proportion of time spent feeding decreased. These results demonstrate that knots recognize variations in the level of predation threat, and adjust their anti-predator responses accordingly. Furthermore, model Sparrowhawks were introduced into the experimental arena at similar distances to the knots, which suggests that knots are able to use cues other than distance to predator to gauge the immediate level of threat a predator poses.

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INTRODUCTION

To reduce their probability of being depredated, animals engage a suite of behaviours including increasing group size and vigilance levels, and altering habitat usage (Caro, 2005). However, increased investment in anti-predator behaviours often comes at a cost, because it reduces the time available for, or efficiency of, other behaviours such as foraging, mating or territory defence (Lima & Dill 1990, Caro 2005). Consequently, when determining their allocation to anti-predator behaviours, prey must balance the conflicting demands of successfully avoiding predators and carrying out other fitness enhancing behaviours (Ydenberg & Dill 1986).

The threat-sensitive predator avoidance hypothesis suggests that prey should match the intensity of their anti-predation response to the degree of immediate threat posed by the predator (Helfman 1989). Empirical studies have confirmed that in a wide variety of taxa, prey do perceive differences in the level of predation danger and adjust their anti-predation responses accordingly (Ydenberg & Dill 1986, Helfman 1989, Lima & Dill 1990, Bulova 1994, Helfman & Winkelman 1997, Laurila *et al.* 1997, Kats & Dill 1998, Persons & Rypstra 2001). Prey may recognize that different species or classes of predator differ in the threat they impose (Caro 2005), or may adjust their behaviour according to differences in habitat structure which influence their ability to detect or escape from predators (Lima & Dill 1990, Caro 2005).

Prey may also distinguish between threatening and non-threatening encounters with individuals of the same predator species. One measure of predation threat is distance, with predators further away imposing less threat than predators nearer to the prey (Ydenberg & Dill 1986). Consistent with this, many animals show increased antipredator response with decreasing distance to predator (Hatch 1970, Helfman 1989, Cavanagh & Griffin 1993, Kleindorfer *et al.* 2005, Welbergen & Davies 2008). For example, in Reed Warblers (*Acrocephalus scirpaceus*), the rate of repetition of alarm calls increases with decreasing distance between the nest of the calling individual and the predator (Welbergen and Davies 2008).

There is also evidence that prey are able to recognize more subtle cues of predator lethality, including auditory, chemical, or postural cues (Caro 2005). For a given predator species, not all individuals are equally lethal. Both Harbour Seals (*Phoca vitulina*) and California Ground Squirrels (*Spermophilus beecheyi beecheyi*) recognize acoustic features of their predators that indicate the degree of threat they impose (Swaisgood *et al.* 1999, Deecke *et al.* 2002). Because predatory individuals are not engaged in hunting all the time, the same individual may not be equally dangerous at all times. Predator behaviour may provide cues as to the current level of threat they impose (Stankowich & Coss 2007). Although several studies have shown that antipredator responses vary in relation to the behaviour exhibited by the predator (Robinson 1980, Helfman 1989, Helfman & Winkelman 1997, Edelaar & Wright 2006, Stankowich & Coss 2007), predator behaviour and distance to the prey are often confounded (Cavanagh & Griffin 1993), making it unclear whether prey are using the behaviour of predators or the distance to predators to assess predation risk.

Here, we use a controlled indoor experiment to investigate the anti-predator behaviour of Red Knots (*Calidris canutus*) towards a representative of a major class of predators, the Sparrowhawk (*Accipiter nisus*). We assessed the general response to increased predation risk by comparing the behaviour of knots when no predators were present (control phase) with their behaviour during a period where they experienced two encounters with Sparrowhawk models each day (experimental phase). We also investigated whether the behavioural response of knots differed according to more subtle variations in predation threat, while controlling for distance to predator. Each day during the experimental phase, knots were exposed one time each to a perching Sparrowhawk model (low threat) and a gliding Sparrowhawk model (high threat). We predicted that knots would show a stronger anti-predation response to the gliding Sparrowhawk model, since this was meant to simulate an attack, and should be perceived as more dangerous than a perching Sparrowhawk.

METHODS

Study subjects

Fifty knots were captured using mistnets on the mudflats of Richel 53°16'57"N, 05°23'82"E and Simonszand 53°29'28"N 06°24'19"E, in the Wadden Sea, The Netherlands, on 8 August and 3 September 2005. Prior to experiments, the birds were housed in aviaries at the Royal Netherlands Institute for Sea Research (NIOZ) in four flocks of 12 to13 birds. The aviary dimensions were 3.85 m by 1.85 m and 2.40 m high, and both temperature and photoperiod were set by prevailing conditions. The aviary floors were kept wet with a constant stream of seawater. A tray of running freshwater for drinking and bathing was always present, and the Mudsnail, *Hydrobia ulvae*, was provided *ad libitum*. Prior to experiments, unique combinations of 1 to 4 colour flags were applied to the lower legs of all individuals (Barter & Rush 1991). All birds appeared to be in good condition following the experiments, and were released into the wild during low tide at a mudflat near the experimental facility. The experiments complied with Dutch law regarding animal experiments (Dutch animal ethics committee licence NIOZ 04.04).

Experimental setup

The experiments took place from 21 August through 28 November 2005 at the indoor mudflat facility of the Royal Netherlands Institute for Sea Research (7 by 7 m and 3.5 m high). A schematic layout of the experimental mudflat is provided in figure 8.1. During the experiments, a constant photoperiod was implemented (lights on from 0600h to 2100h), with 'moonlight' mimicking illumination being provided during the dark phase.

We carried out 8 trials on flocks of 6 randomly selected birds. Each trial consisted of a 2 day habituation period, followed by a 5 day control and a 5 day experimental period. The order of experimental and control periods was determined

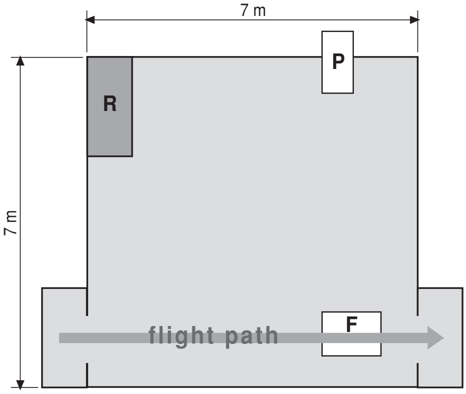

Figure 8.1 Schematic representation of the experimental arena. The dotted line with arrow indicates the flight path of the gliding Sparrowhawk model. The area where the perched Sparrowhawk entered the mudflat (P), the location of the food tray (F), and the location of the roosting platform (R) are also indicated.

at random for each flock, with 4 flocks receiving the experimental period first, and 4 flocks receiving the control period first.

During the experimental period of the trials, two event types were used to elevate predation threat. The first consisted of the gliding Sparrowhawk model accompanied by digital recordings of Red Knot alarm calls. The stuffed model glided across one end of the mudflat, passing over the food tray (figure 8.1). Gliding events lasted circa 5 s. The second event type involved presenting a model of a perched Sparrowhawk supplied with a built-in electromotor which allowed head movement. The perched Sparrowhawk model was hidden behind a black curtain except during 'perching' events, when the curtain was lifted and the perched model was rolled into the mudflat arena for 1 min, approximately 0.5 m above the mudflat surface. During the experimental period, 'gliding' and 'perching' events were carried out once each day at unpredictable times between 0930h and 1700h with the constraint that events not occur within 90 min of each other in order to allow sufficient time for focal observations between events (see below).

Adopting a set-up with a blank control and two intrusion event types within the experimental treatment, enabled testing for discriminatory abilities of prey by comparing three levels of threat: very low threat (control), low threat (perched Sparrowhawk model) and high threat (gliding Sparrowhawk model).

In order to clean the mudflat, during all phases of the trials (i.e.: habituation, control and experimental), it was flooded briefly with sea water (for between 10 and 30 min) at 1800h. During this time, the birds could rest on an elevated roosting platform. Food was also replaced at this time. Trays of *Hydrobia* were provided in sufficient quantity to allow *ad libitum* feeding for the following 24h (see below for additional information on food).

Behavioural observations

Five minute continuous focal observations were made of each flock member 4 times per day during both the control and experimental phases of the experiments. Observations were carried out before and after each of the predator events during the experimental period, and at matching time periods during the control period. The order of observation of individuals was randomized. Focal observations were made from behind a 1-way mirror, dictated into a microcassette recorder, and later transcribed using The Observer 3.0 Event Recorder (Noldus Information Technology, Wageningen, the Netherlands). All observations were carried out by KJM.

We recorded 4 behavioural categories (feeding, searching, vigilance, and 'others'). Birds were considered to be foraging only when pecking in the food tray. Pecking on the mudflat away from the food tray and walking with the head oriented downwards were both categorized as searching. Vigilance was defined as the bill being parallel to the horizon or higher with accompanying side to side movement of the head. 'Others' includes all behaviours not described above, but most often consisted of resting (motionless with the head up), roosting and preening. Also, following each predator event, the duration of the escape flights was recorded for each bird, as was latency to resume feeding (up to a maximum of 90 min).

Estimated food consumption

Throughout the experiments, knots were fed with *Hydrobia* that were caught on 30-31 May 2005 near the Afsluitdijk, The Netherlands (52°58'07"N, 05°06'06"E). *Hydrobia* were stored frozen at –20°C, and thawed immediately before use. The total wet mass of food provided each day was calculated as the difference between the mass of the feeding tray after filling with *Hydrobia* and the mass of the empty food tray. In order to estimate the total ash free dry mass (AFDM) of the food provided, 3 subsamples (circa 60 g each) were collected and weighed (wet mass or WM). The subsamples were then dried at 60°C to constant mass (range 4 to 7 d), weighed (dry mass or DM), and then burned at 560°C for 4 h and re-weighed (ash mass or AM). AFDM of each subsample was calculated as DM-AM. Based on the mean ratio of AFDM:WM of the three subsamples, we calculated the ADFM of the food tray provided.

All food remaining on the food tray after 24 h was collected and weighed at 1800h each day. The entire sample was collected, weighed, dried, and burned as described above. Because some of the *Hydrobia* meat would be lost via decay over the 24 h period, changes in the AFDM of *Hydrobia* ($AFDM_{provided}$-$AFDM_{remaining}$) are overestimates of actual consumption by the knots, but provide an index of relative consumption. 3 samples were lost before processing, yielding a total of 77 estimates of daily food consumption.

Statistical analyses

For each focal observation, we calculated the proportion of time spent vigilant, the mean scan duration (s), mean scanning rate (scans min^{-1}), the proportion of time spent feeding, and the proportion of time spent searching for food. In the experimental phase of experiments, we also calculated the duration of escape flights (s), and the proportion of individuals resuming feeding within 90 min of hawk events.

Data were analysed using linear mixed effects models (LMEs). LMEs provide estimates of the influence of fixed effects on the mean as well as the influence of random effects on the variance, thereby accounting for the non-independence of errors resulting from the repeated measures on individuals as well as the repeated measures within flocks (Pinheiro & Bates 2000). LMEs were constructed using R v.2.6.1 ('lme' function of the 'nlme' package of the R statistical computing environment). We tested for differences in escape flight duration between the two hawk event types using models with 'event type' as a fixed effect, and treatment order, flock within treatment order, id within flock within treatment order, and day within id within flock within treatment order as random effects (~1| treatment order/flock/id/day). Differences in the proportion of individuals resuming feeding within 90 min of a predator event were analyzed in the same manner; with the exception that 'id' was not included in the random effects term.

We tested for the effect of predator events on vigilance and foraging behaviour of Red Knots by including 'treatment' (control or experimental), 'event type' (hawk gliding event or hawk perching event), and observation period (before or after the hawk event) as well as their interactions as fixed effects in the model. 'Event type' was used as a sham factor in the control phase of the experiment in order to account for the fact that observation times in the control and experimental phase of the experiment were matched for time of day. The random effects structure was the same as described above (~1| treatment order/flock/id/day). Finally, we tested for an effect of treatment on total daily food consumption using 'treatment' as a fixed effect, and the following structure for random effects (~1| treatment order/flock/ day).

For all models, non-significant interactions ($P > 0.10$) were removed in a reverse stepwise manner. We used a significance threshold of 0.10 for interactions because statistical tests have reduced power to detect significant interactions (Littell *et al.* 1991). We interpreted the significant interactions in lme's based on the effects sizes estimated by the model (Pinheiro & Bates 2000). All proportions data were arcsine square root transformed prior to analyses to normalize their distributions. Data on escape flight duration, mean scan duration, and scanning rates were Poisson distributed. Therefore, we used ln (n+1) transformations to normalize their distributions prior to analyses.

RESULTS

Red Knots responded immediately to predator events with escape flights (range 0 to 116 s). Escape flights were significantly longer following hawk gliding events (34.73 ± 1.27 s) compared with hawk perching events (28.21 ± 1.27 s) ($F_{1,239} = 63.92$, $P < 0.001$).

Predator events also produced several changes in the activity budgets of Red Knots. All three indices of vigilance (proportion of time spent vigilant, mean scan duration, scanning rate) showed changes according to event type, observation period, and treatment (see Table 8.1 and Fig. 8.2A). During the control phase, the proportion of time spent vigilant varied between less than 0.3 to greater than 0.6.

There were no consistent effects of event type or observation period on these changes however. The proportion of time spent vigilant was higher during the experimental phase (range 0.6 to 0.9). During the experimental phase, the proportion of time spent vigilant also increased following hawk gliding events, but not following hawk perching events.

Similar results were observed for mean scan duration (Table 8.1 and Fig. 8.2B). During the control phase, variation in mean scan duration was not related to either event type, or observation period. Again, overall scan durations were higher during the experimental phase. Scan duration increased following hawk gliding events, but

Table 8.1 LME results for measures of vigilance: proportion of time spent vigilant, scanning rate (scans/min) and mean scan duration (s). All data were transformed prior to analyses in order to normalize their distributions.

Source of Variation	Effect size	SE	df	F	*P*
A. Dependent variable: arcsine sqrt (proportion of time spent vigilant)[a]					
Treatment[†]	0.54	0.03	1	383.27	<0.0001
Event type[‡]	0.01	0.03	1	3.39	0.066
Observation period§	0.13	0.03	1	0.20	0.66
Treatment[†] × Event type[‡]	–0.20	0.05	1	3.43	0.064
Treatment[†] × Observation period[§]	–0.39	0.05	1	57.79	<0.0001
Event type[‡] × Observation period[§]	–0.03	0.05	1	13.55	0.0002
Treatment[†] × Event type[‡] × Observation period[§]	0.28	0.06	1	20.03	<0.0001
B. Dependent variable: ln (scans per min + 1)[b]					
Treatment[†]	–0.03	0.00	1	62.63	<0.0001
Event type[‡]	0.01	0.00	1	19.94	<0.0001
Observation period[§]	0.01	0.00	1	29.08	<0.0001
Treatment[†] × Event type[‡]	0.01	0.01	1	0.14	0.71
Treatment[†] × Observation period[§]	0.03	0.01	1	15.16	0.0001
Event type[‡] × Observation period[§]	0.00	0.01	1	14.60	0.0001
Treatment[†] × Event type[‡] × Observation period[§]	–0.02	0.01	1	7.98	0.0048
C. Dependent variable: ln (Scan duration (s) + 1)[c]					
Treatment[†]	1.67	0.10	1	386.38	<0.0001
Event type[‡]	–0.22	0.10	1	20.05	<0.0001
Observation period[§]	0.04	0.10	1	45.25	<0.0001
Treatment[†] × Event type[‡]	–0.62	0.14	1	0.88	0.35
Treatment[†] × Observation period[§]	–1.35	0.14	1	73.87	<0.0001
Event type[‡] × Observation period[§]	0.11	0.14	1	45.59	<0.0001
Treatment[†] × Event type[‡] × Observation period[§]	1.06	0.19	1	30.09	<0.0001

[†] 'Control' was the reference for Treatment in the model

[‡] 'Gliding' was the reference for Event type in the model

[§] 'Post-' was the reference for Observation period in the model

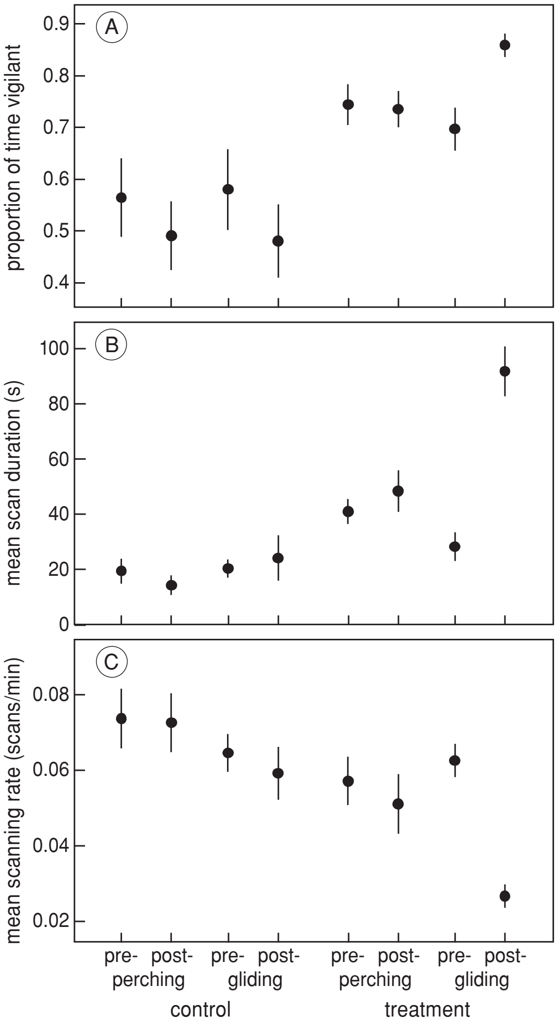

Figure 8.2 Changes in A) proportion of time devoted to vigilance, B) mean scan duration, and C) mean scanning rate in relation to treatment, event type and observation period. Note that raw values are depicted, while models were constructed for transformed data. Values indicated are means ± 1 se.

there was no change in mean scan duration following hawk perching events. Changes in scanning rate were opposite to changes in mean scan duration. Again, there was no consistent effect of event type, or observation period on scanning rates during the control phase. During the experimental phase, scanning rates did not change following hawk perching events, but decreased following hawk gliding events.

Knots also avoided feeding following predator events (range 11 to > 90 min following hawk gliding event, 1 to > 90 min following hawk perching event). However, the proportion of birds feeding within 90 min of a hawk perching event was nearly double the proportion feeding within 90 min of a hawk gliding event (0.76 ± 0.08 versus 0.42 ± 0.08, respectively), and this difference was significant ($F_{1,39} = 27.24$, $P < 0.001$).

The reduced tendency to feed was also reflected in the amount of time devoted to feeding and searching for food on the mudflat (away from the food tray) (Table 8.2). Overall, the proportion of time spent feeding was lower during the experimental phase than during the control phase (mean difference 0.04 ± 0.00) (Fig. 8.3A). During the experimental phase, birds also reduced the proportion of time spent feeding following predator events, with a larger decrease observed following hawk gliding events than hawk perching events. During the control phase, there was no effect of observation period or event type on the proportion of time spent foraging.

Results for the proportion of time allocated to searching were similar. Overall, birds spent less time searching during the experimental phase compared with the control phase (Table 8.2, Fig. 8.3B). During the experimental phase, birds reduced the proportion of time spent searching for food following hawk gliding events, but not following hawk perching events. In contrast, during the control period, there was no effect of observation period or event type on the amount of time spent searching.

The reduced time feeding and searching for food resulted in changes in food consumption during trials. Knots consumed significantly less during the experimental phase ($F_{1,36} = 12.87$, $P = 0.001$). The average food consumption during the control phase was 164.40 ± 7.06 g AFDM, compared with 139.72 ± 9.86 g AFDM, a mean reduction of 15%.

Table 8.2 LME results for proportion of time spent feeding and proportion of time spent searching for food outside the food tray. Proportion data were transformed prior to analyses to normalize their distributions.

Source of Variation	Effect size	SE	df	F	*P*
A. Dependent variable: arcsine square root (proportion of time feeding)					
Treatment†	–0.21	0.02	1	158.15	<0.0001
Event type‡	0.06	0.02	1	9.27	0.0024
Observation period§	0.04	0.02	1	55.71	<0.0001
Treatment† × Event type‡	0.04	0.03	1	2.44	0.12
Treatment† × Observation period§	0.19	0.03	1	31.50	<0.0001
Event type‡ × Observation period§	–0.03	0.03	1	22.00	<0.0001
Treatment† × Event type‡ × Observation period§	–0.14	0.04	1	10.50	0.0012
B. Dependent variable: arcsine square root (proportion of time spent searching)					
Treatment†	–0.09	0.01	1	151.84	<0.0001
Event type‡	0.07	0.01	1	16.37	0.0001
Observation period§	0.04	0.01	1	14.67	0.0001
Treatment† × Event type‡	–0.02	0.01	1	2.76	0.097
Treatment† × Observation period§	0.04	0.01	1	6.91	0.0086
Event type‡ × Observation period§	–0.06	0.01	1	16.09	0.0001

† 'Control' was the reference for Treatment in the model
‡ 'Gliding' was the reference for Event type in the model
§'Post-' was the reference for Observation period in the model

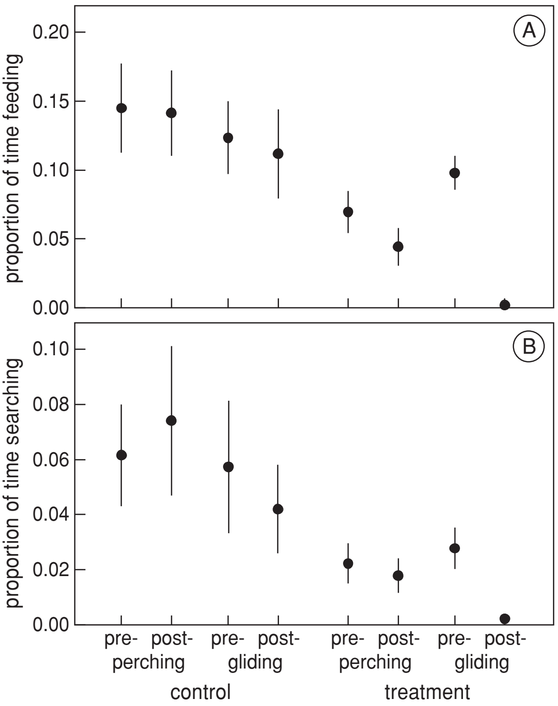

Figure 8.3 Changes in the proportion of time spent A) feeding and B) searching, in relation to treatment, event type and observation period. Note that raw values are depicted, while models were constructed for transformed data. Values indicated are means ± 1 se.

In each of the models presented above, the random effect of 'day' accounted for a large proportion of the variation in the data sets. In contrast, 'treatment order' had a consistently small effect, indicating that the response of Red Knots to our treatments was not conditional on the order in which they received the treatment phases. Variance components for all random effects are summarized in Table 8.3.

Table 8.3 Variance components for model random effects. For details of model fixed effects, see Tables 8.1 and 8.2.

Model dependent variable:	Treatment order	Group	ID	Day
Arcsine square root (Prop time vigilant)	0.00	10.94	3.87	82.09
Ln (Scanning rate (scans / min) + 1)	1.03	0.11	5.71	90.51
Ln (Scan duration (s) + 1)	0.00	5.62	4.90	87.08
Arcsine square root (Prop time feeding)	0.00	6.42	4.09	84.26
Arcsine square root (Prop time searching)	0.00	10.49	5.22	80.10
Ln (Escape flight duration (s) + 1)	0.00	27.20	0.00	72.80
Arcsine square root (Prop resuming feeding)	0.00	8.59	N/A	57.11
Food consumption (g)	5.51	0	N/A	94.49

DISCUSSION

We tested whether Red Knots adjust the intensity of their anti-predation response according to the degree of threat posed by predators by comparing their behaviour across three levels of predation threat: no predators present (very low predation threat), presentation of a perching Sparrowhawk model (low predation threat), and presentation of a gliding Sparrowhawk model (high predation threat). In all behavioural parameters measured (escape flights, vigilance, and feeding), Red Knots appeared to discriminate between the different levels of predation risk. The presence of the Sparrowhawk model prompted escape flights by the knots, and the duration of escape flights was longer following the gliding Sparrowhawk events compared with perching events. Predator events also resulted in an increased proportion of time spent vigilant, and a decreased proportion of time spent feeding. The magnitude of these effects was greater following gliding Sparrowhawk events.

Knots responded immediately to the presence of Sparrowhawks in the experimental mudflat with escape flights. Distance moved is a commonly used metric to assess a prey's perception of predation risk (Taylor & Knight 2003, Stankowich 2008), with greater distance moved being associated with higher perceived predation risk. However, because the knots were confined to the experimental mudflat, the net distance they could move was restricted. Therefore, we recorded the duration of escape flights following predator events because the duration of escape behaviour has also been shown to correlate with perceived predation risk (Nebel & Ydenberg 2005, Stankowich & Coss 2007). Escape flights were longer following the gliding Sparrowhawk events compared with perching events, results that are consistent with Red Knots perceiving the hawk gliding events as imposing a greater level of threat than the perching events.

Following hawk gliding events, knots increased the proportion of time spent vigilant. Their patterns of vigilance also changed, with vigilance bouts lasting longer, but occurring less frequently following hawk gliding events. In contrast, there was no change in the time allocated to vigilance following hawk perching events, although knots did alter their vigilance strategy following hawk perching events. As with hawk gliding events, scan duration increased and scanning rate decreased following hawk perching events. However, these trends were of smaller magnitude compared with hawk gliding events.

Encounters with predators often result in an immediate interruption of feeding behaviour (Lima & Dill 1990). Latency to resume feeding can depend on a variety of factors, including the hunger level of the prey, but is also strongly influenced by predation danger (Lima & Dill 1990, Caro 2005), with latency to resume feeding increasing with increased perceived predation danger (Lima & Dill 1990, Cooper 1998, van der Veen 2002, Martín & López 2005). More birds resumed feeding within 90 min of a hawk perching events (>75%) compared with hawk gliding events (~ 40%). These results therefore suggest that knots perceived the gliding hawk events as imposing a greater threat than the perching hawk events. Alternative explanations, such as hunger level, are unlikely to account for these results because there should be no systematic differences in hunger level associated with the two predator event types given that event types and times were randomly assigned.

The results of latency to resume feeding are also reflected in the analyses of the proportion of time spent feeding. While knots reduced their investment in feeding behaviour following both types of predator events, the reduction was greater following hawk gliding events. These results are also consistent with knots perceiving a gliding hawk as a greater predation threat than a perched Sparrowhawk. Alternatively, the greater aversion to feeding following hawk gliding events may not reflect an aversion for the behaviour itself, but may be the result of avoidance with the location in the experimental arena where the food tray was located, because it lay under the flight path of the gliding Sparrowhawk. However, the proportion of time spent searching for food outside of the food tray showed very similar patterns to those for feeding, suggesting that the reduction in feeding was not merely a consequence of avoiding the location where the food tray was located, but did in fact reflect a reduced tendency to forage.

Behavioural changes induced by encounters with predators may not be long-lasting, in which case, observations of behaviour immediately following predator events may provide overestimates of the long-term effect of predators on the behaviour of prey (Lima & Bednekoff 1999). Our results do show strong immediate responses to predator events, particularly following hawk gliding events. However, comparisons of behavioural measures prior to encounter with predators during the experimental phase, and all measures taken during the control phase, indicate that there were also long-term changes in the behaviour of knots induced by encounters with predators. Overall vigilance levels (proportion of time spent vigilant and mean scan duration) were greater during the experimental phase, and both proportion of time feeding and proportion of time searching were lower. Measures of food consumption throughout the trials confirm that the reduction in feeding behaviour was lasting in the experimental phase. Although predator events lasted less than 2 min out of a 15 h foraging period, they resulted in a 15% reduction in food consumption during the experimental phase.

One possible criticism of our experimental design is that the control phase did not provide a true control. The hawk events during the experimental phase not only increased perceived predation danger, but also created a disturbance, and Red Knots are known to be sensitive to disturbances (Koolhaas *et al.* 1993, McGowan *et al.* 2002). However, under natural conditions, encounters with predators would provide both a disturbance and an increased perceived risk of predation to prey; therefore, we believe our design does provide meaningful estimates of the response of knots to encounters with predators. In a similar study, van den Hout *et al.* (2006) compared the anti-predation response of Ruddy Turnstones (*Arenaria interpres*) to a raptor model versus a gull model. They found that the gull model had no consistent effect on the turnstones relative to their starting values prior to the experiments, while the raptor model had a strong effect. These results suggest that the major factor driving the response in the prey is increased perceived predation risk, and not disturbance. Furthermore, in our study, the duration of the hawk perching events (1 min) greatly exceeded the duration of the hawk gliding events (circa 5 s). Thus, even if knots are more sensitive to disturbance than turnstones, the greater response of Red Knots to hawk gliding events cannot be explained by greater levels of disturbance associated with those events, but is consistent with the gliding Sparrowhawk events being perceived as more threatening than perching Sparrowhawk events.

The investment in vigilance behaviour was high throughout the experiments, including the control phase which was meant to simulate very low predation threat. This may be due to easy access to *ad libitum* food, freeing up more time for vigilance behaviours. However, the high levels of vigilance may also have been due to knots having had high perceived danger throughout the experiment, including the control phase, which may have resulted either from the daily disturbances knots experienced when food was replenished and the mudflat was cleaned, or from the structure of the experimental mudflat. Shorebirds are often hunted by predators which rely on obstructive cover to conceal their attacks (Lazarus & Symonds 1992, Pomeroy *et al.* 2006). The walls surrounding the experimental mudflat may have been perceived as providing obstructive cover for such predators.

Our results show graded responses by Red Knots to increasing levels of predation danger. Previous studies have suggested that prey are able to use the behaviour of predators to gauge predation risk, however, studies in birds have often confounded predator behaviour and distance to predator (Hatch 1970, Cavanagh & Griffin 1993, Edelaar & Wright 2006). In our study, the stronger responses to the gliding predator events cannot be explained by proximity between the knots and the Sparrowhawk model, because the experimental arena was relatively small arena (7 by 7 m), and distances between the knots and the predators during the two event types were similar. Thus, knots were able to use cues other than distance to evaluate predation risk. The 'high threat' gliding events were accompanied by recordings of Red Knot alarm calls. Therefore, we cannot conclude to what extent the behaviour of the gliding Sparrowhawk versus the presence of alarm calls contributed to the increased perception of risk. Nonetheless, our results clearly demonstrate that knots do recognize variations in the level of predation threat, and adjust their anti-predator responses accordingly.

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We are very grateful to Maarten Brugge and the crew of HM *Navicula* for help with catching the experimental Red Knots and for fishing Mudsnails with us. We thank two anonymous referees for their comments on an earlier version of this paper. During the writing of the manuscript, KJM was supported by an NSERC scholarship and an NSERC discovery grant to Luc-Alain Giraldeau. The experiments complied with Dutch law regarding animal experiments (Dutch Animal Ethics Committee-licence NIOZ 04.04).

BOX V

Escape decisions: trade-offs between energy and safety prospects

Piet J. van den Hout

INTRODUCTION

Birds typically respond to attack by escape flight. Predators often use obstructive landscape structures to decrease detection opportunities by prey as much as possible. Yet, detection is not always followed by immediate escape. Apart from the option to stay put, which may be a good way of avoiding attack by Peregrine *Falco peregrinus*, which may be reluctant to take prey from the ground (Cresswell 1993), birds may just delay escape flight for some reason. This implies that differences in time delay between flight responses – or alarm calls for that matter – in response to attack may not be taken as evidence for differences in attentiveness (Ydenberg & Dill 1986).

Fleeing entails costs, such as the relatively high costs of short flight (Hambly *et al.* 2004) and loss of feeding opportunity, which birds should trade-off against the cost of remaining in place, which may involve the chance of getting killed. The latter may depend on, for instance, escape destination. Passerines that escape into vegetation may be more inclined to forage longer before deciding to flee when they are closer to that bush, their escape destination. Alternatively, birds that lack such an escape destination, such as many shorebird species that forage on exposed mudflats, may use other escape tactics such as socially-coordinated escape. For such species the proximity of recruits for coordinated escape flight may guide their escape decision (Chapter 9 in this thesis). In any case, the extra feeding time gained by not fleeing should compensate for the increased risk of capture, and thus we expect this to depend on the state of the animal. This should equally apply to the resumption of feeding after attack.

FIELD OBSERVATIONS

In their wintering area, on the Banc d'Arguin, Mauritania, while tallying age-proportions in flock of Red Knots foraging at incoming tide on near-shore seagrass beds (see Chapter 5), from time to time such flocks were disturbed by raptors attacks. In 21 of such occasions I had just finished such a flock composition assessment, which gave me the chance to compare this to the flock size and composition of birds that foraged on the site immediately after the disturbance (I use disturbance, not attack, as I could not determine which of the remaining individuals had actually been targeted or just disturbed).

RESULTS

Obviously, flock size shortly after disturbance was much smaller, as most birds had left the area either to return after a couple of minutes or longer, or to leave to another foraging patch, or else for the roost and stay there until receding tide. More strikingly, shortly after the disturbance the relative abundance of juveniles nearshore was much higher than before, indicating that juveniles have a higher propensity to stay or at least resume feeding shortly after disturbance (Figure V.1).

DISCUSSION

I will speculate as to possible explanations for the fact that juveniles have a lower tendency to flee from predators. First, individual difference in the prospects of successful escape might explain the observation. If juveniles would be less skilful in coordinated flockwise escape flights, the prospects for safety by fleeing would be less favorable for them than for adult conspecifics, so costs of fleeing are high (F_{high} in Fig. V.2). This would make them less inclined to flee (dependent of the cost of

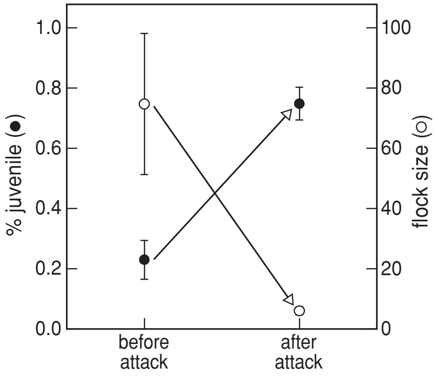


Figure V.1 Flight propensity after disturbance by a raptor, showing that juveniles are less inclined to flee and/or have higher propensity to resume feeding immediately after disturbance than adults.

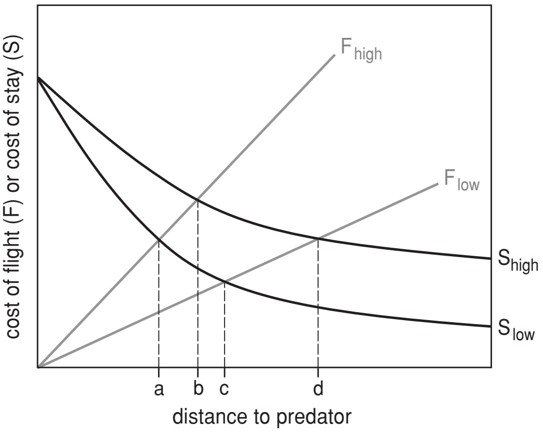
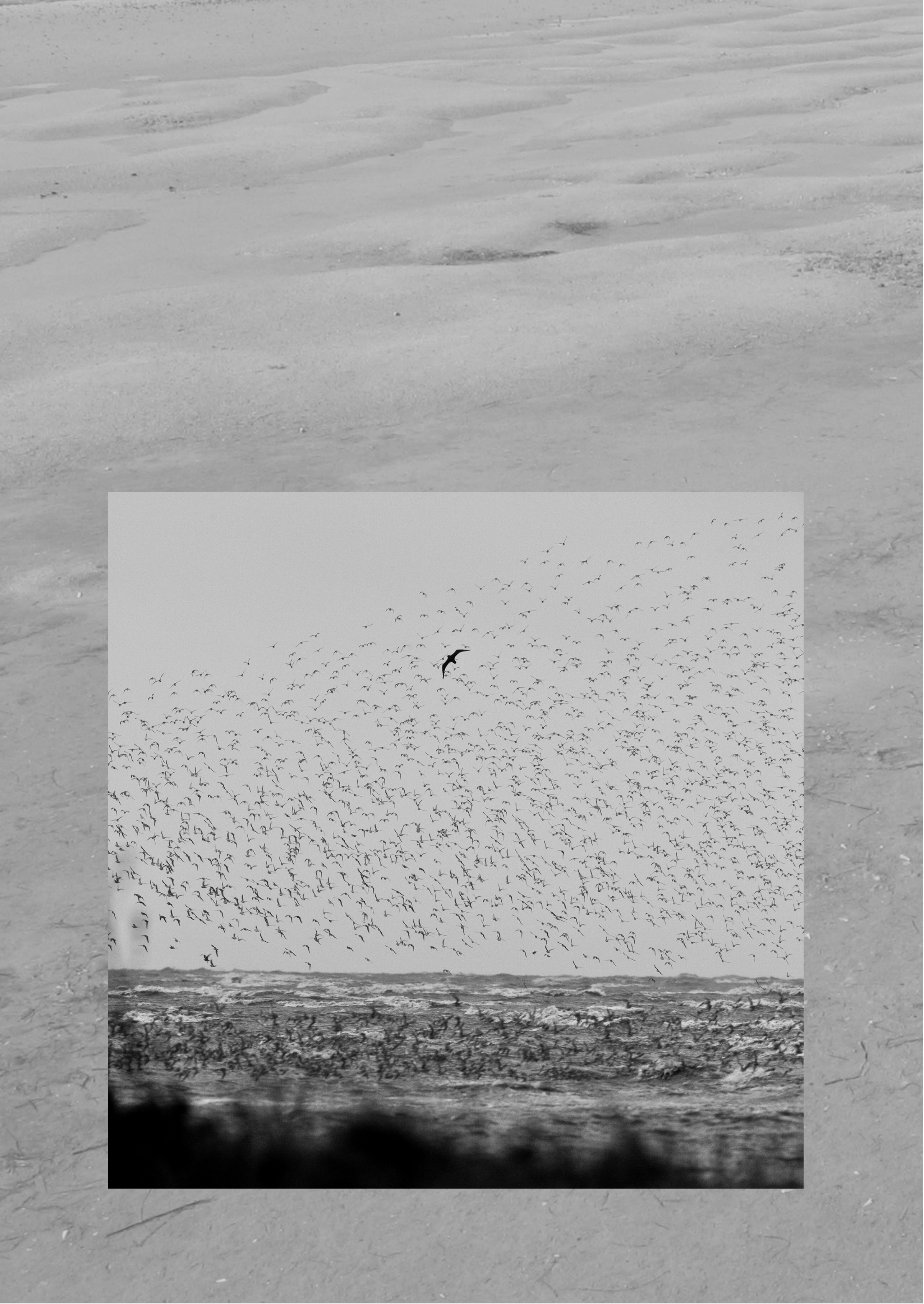


Figure V.2 Graphic illustration of the costs of fleeing (F) and staying (S) for poor foraging juveniles and good foraging adults. See text for explanation. (Adapted after (Ydenberg and Dill, 1986).

staying – see further on – the option for juveniles would be (a) or (b)). The propensity to stay put could even be the result of juveniles foraging at the edge of a flock, which would make them less able to quickly merge with conspecifics in socially-coordinated escape flight.

An alternative explanation, though not incompatible with the former, would be that these juveniles are poor foragers, which due to a low energy state, are less willing to give up feeding opportunity for escape (an interpretation that would correspond with the results as presented in Chapter 5). Thus, juveniles would have lower cost of staying (S_{low}) which corresponds to a lower tendency to flee with an approaching raptor (dependent of the costs of fleeing, this would yield options (a) or (c)). Of course, both mechanisms could work together, and this would yield (a) as the appropriate option for juveniles in case both cost of staying were low and cost of fleeing were high.

In conclusion, an immediate escape upon detection of a predator does not have to be the optimal response. The optimal escape decision may be subject to individual abilities in foraging and sociality. Finally, as detection does not necessarily lead to an immediate escape response, a delay in response cannot per definition be regarded as a delay in detection. In other words, the recognition or detection phase must be separated from the pursuit or escape phase (Caro 2005; Vermeij 1982). This has to be taken into account when interpreting results of vigilance studies that link for example response time to flock size and corresponding detection potential (Ydenberg & Dill 1986).



CHAPTER 9

Predator escape tactics in birds: linking ecology and aerodynamics

Piet J. van den Hout, Kimberley J. Mathot, Leo R.M. Maas and Theunis Piersma

ABSTRACT

In most birds, flight is the most important means of escape from predators. Impaired flight abilities due to increased wing loading may increase vulnerability to predation. To compensate for an increase in wing loading, birds are able to independently decrease body mass or increase pectoral muscle mass. Comparing nearshore and farshore foraging shorebird species, we develop a theory as to which of these responses should be the most appropriate. We hypothesize that nearshore foragers should respond to increased predation by increasing their pectoral muscle mass in order to promote speed-based escape. Instead, farshore foragers should decrease body mass in order to improve agility for maneuvering escape. Experiments on two shorebird species are consistent with these predictions, but on the basis of the theoretical framework for evaluating effect size and biological significance developed here, more experiments are clearly needed.

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INTRODUCTION

Hunting and escape strategies of predators and prey are probably the result of a coevolutionary arms race (Dawkins 1999). Yet, this interaction is asymmetric. An individual prey has more to lose by failure to avoid a predator than predators by failing to catch a prey. Therefore, selection pressures to avoid being killed should be particularly strong for prey species.

Animals respond to approaching predators in many ways. They can startle the predator, stand their ground, crouch and stay put, or fly off (Caro 2005). For most birds, flight is the predominant escape mode. A reduction of speed or maneuverability is likely to increase the chance of being predated once airborne (Howland 1974, Witter *et al.* 1994). Although it has become widely acknowledged that escape flight performance is influenced both by the muscle power available for fast forward flight and movements and by wing loading (i.e. the body mass/wing surface ratio) (Howland 1974, Hedenström & Alerstam 1992, Hedenström & Rosén 2001, Videler 2005), most experimental studies to date have investigated the effect of wing-loading on flight performance without measuring possible compensation for flight capacity by changes in pectoral muscle size (Lima & Valone 1986, Witter *et al.* 1994, Gosler *et al.* 1995, Lima 1995, Kullberg *et al.* 1996, Lilliendahl 1997, Carrascal & Polo 1999, Lilliendahl 2000, Burns & Ydenberg 2002, Kullberg *et al.* 2002; but see Lind 2001). However, there is evidence that compensation for flight capacity changes are possible: during migration birds have been shown to adjust the size and capacity of specific body parts (Piersma & Drent 2003) including rapid reversible adjustments of pectoral muscle relative to body mass levels (Lindström *et al.* 2002, Dietz & Piersma 2007). Furthermore, by experimentally inducing molt gaps, Lind & Jakobsson (2001) demonstrated that pectoral muscle size and body mass can be independently regulated in response to wing loading. Such fine-tuning can additionally be influenced by predation danger (van den Hout *et al.* 2006).

When discussing body composition adjustments to predation danger, we must distinguish between, on the one hand, the mode of adjustment (adjustment in either overall body mass or pectoral muscle mass, or a combination of both), and, on the other hand, the sensitivity to fuel load in terms of predation costs, that is, the extent to which a decrease in flight performance affects predation danger. While a change in mass components may be advantageous in terms of flight performance, it will involve costs. For instance, a reduction in body mass, though improving flight performance, also increases the risk of starvation (McNamara & Houston 1990, Witter & Cuthill 1993). Therefore, responses to predation threat are expected to reflect a trade-off between the benefits and costs of changes in body mass components (Witter *et al.* 1995). The amount of energy stores that a bird is willing to sacrifice may depend on the predation costs that the corresponding extra body mass would entail. Predation costs include the extent to which the negative impact of fuel load on flight performance affects survival probability. Lind (2004) argued that the importance of flight performance for predation danger increases as the distance from protective cover increases, because small increases in wing loading have little effect on escape chances on such small distances (Lind *et al.* 2004). Generally, mass-dependent predation costs may be lower for species that can feed close to protective cover than for species that forage in areas devoid of protective cover (Dierschke 2003; Lank & Ydenberg 2003).

Birds living in open habitats, on mudflats for example, may be particularly sensitive to fuel load in terms of predation costs. For such habitats, vegetation and other topographical structures are not perceived as safe havens, but rather as obstructive cover, as these allow an undetected approach by predators (Piersma *et al.* 1993, Cresswell 1996). Vertical habitat structures will generally be avoided (Zwarts 1988, Rogers *et al.* 2006). However, due to their foraging specializations, some species are forced to forage close to the shoreline, where dunes, dykes or vegetation obstruct their view of the horizon (Metcalfe 1984).

In this paper we compare these nearshore and farshore foraging species. Using aerodynamic theory, we predict differences in their responses to predation in terms of body mass and pectoral muscle mass. We also predict that species-specific morphological responses to predation are not only related to their escape tactic and related ecologies, but may also be reflected in flight frame characteristics. Finally, we discuss molt given that gaps in the wing affect wing loading and may influence the perception of predation danger (Lind 2001), thus mediating phenotypic responses to predation threat. A brief description of how the predictions can be tested will be followed by a discussion of the results of such an experiment.

ESCAPE SCENARIOS: LINKING ECOLOGY AND AERODYNAMICS

The difference between nearshore and farshore escapers is best explained by considering two major generalizations, based on the relative position of prey and predator, speed vectors between prey and predator when the prey detects the predator (Hedenström and Rosén, 2003), and escape destination (Lima 1993).

Nearshore foragers

Shorebird species that tend to forage in the close vicinity of obstructive cover are often confronted with predators at close range, as the physical properties of the habitat supply the predator with opportunities for undetected approach (Metcalfe 1984). Individuals aiming to reach a safe destination, such as water or salt marsh, require a speed-based, accelerating escape (linear maneuverability) in order to reach that destination before the predator strikes. Such speed-based locomotion requires the ability of generating a high velocity of shortening in the locomotor muscles (Kumagai *et al.* 2000), while an increase of such speed-based escape abilities would call for a build-up of fast-twitch muscle fibers (Rosser & George 1986). Such bird species are expected to respond to predation danger by pectoral muscle mass increase, which allows them to save on energy stores.

Measures for wing shape in this context include aspect ratio (wing span^2/wing area) (Warrick 1998, Hedenström & Rosén 2001) and wing tip pointedness/roundedness and convexity (Monkkonen 1995, Lockwood *et al.* 1998, Burns & Ydenberg 2002). The two measures are related: wing pointedness results in a high aspect ratio (Norberg 1989). Bird species employing speed-based escape are expected to have relatively low aspect wing ratios, as the inertia of high aspect ratio wings (which increases with the square of their length) may compromise the mass-specific power output generated by wing-flapping (Warrick 1998). Likewise, such bird species may have rounder wingtips, which are said to maximize thrust from flapping wings (Rayner 1993). Additionally, rounded wings produce relatively more lift towards the wingtip, where the wing is moving faster, but also more drag. These factors are likely to enhance flight performance at low speeds, particularly at take-off from the ground and maneuverability by differential wing-flapping (Swaddle & Lockwood 1998, Warrick *et al.* 1998).

Farshore foragers

The essential difference between the escape context of farshore and nearshore foragers is the distance between prey and predator at the time the prey detects the predator. Farshore foragers typically avoid foraging near obstructive cover (Rudebeck 1950-1951, Brown & Kotler 2007). This allows birds to detect an approaching predator from a relatively large distance, permitting relatively early take-off, and time to gain speed and prepare maneuvers. Gregariousness has additional advantages in this scenario, as high levels of vigilance ('many eyes') combined with an unobstructed view of the horizon, increases the chance of early detection (Krause & Ruxton 2002), and provides time to recruit flock members for a socially coordinated escape. Calidrid species (sandpipers) (Figure 9.1) are well-known for such united, erratic display flights to form flocks which appear to pulsate and maneuver as one organism (Rudebeck 1950-1951, Lima 1993), but time lags between detection and encounter with the predator, allow even relatively solitary foragers to team up with such 'escape units' (pers. obs.).

In such a scenario, turning maneuverability, rather than linear maneuverability, may be of paramount importance. Studies that focus on maneuverability commonly address low speed maneuvering (Warrick & Dial 1998, Warrick *et al.* 1998), and less is known about flight maneuvers that are initiated at high speed. Warrick & Dial (1998) argue that at high speeds, birds can exploit the acquired lift forces to produce angle of attack asymmetries immediately, without preparation (i.e. an upstroke). High aspect ratio wings are most suitable for such maneuvers. "In addition", they write, "by not driving the wings through a downstroke while pronating/supinating, the bird directs most of the lift on the outside wing perpendicular to the roll axis, and could theoretically produce negative angles of attack on the inside wing. The result would be a pure-rotation bank, with the bird rolling around its center of mass at high angular accelerations". This would mean that, at higher speeds, birds can economize on muscle power for wing-flapping, exploiting lift forces for turns. This

Figure 9.1 Photographic illustration of fast pure-rotational banks by Dunlins *Calidris alpina* chased by a Peregrine Falcon *Falco peregrinus*. Note that neither of the birds shows the flapping velocity asymmetries (see text). Instead, pronation/supination of the wing is apparent in most of the birds, particularly by the two closely paralleled birds in the lower-middle of the picture. The photo, found on the World Wide Web, was taken by an anonymous photographer.

is what the sandpipers in Figure 9.1 seem to do. At these high speeds, lift forces on the hand wing are the dominant forces as further from the centre of gravity lever effects on the roll control will be stronger (Videler 2005). Now, inertia properties of the flight frame put limits on the turning radii which the birds can perform when escaping from a predator. This means that through a decrease in body mass alone, birds can decrease turning radii. This can be mathematically demonstrated using aerodynamic theory as follows.

Steady flight in still air requires balanced forces where lift equals weight and thrust equals drag, as well as balanced moments of these forces about the centre of gravity (Videler 2005). Warrick *et al.* (1998) describe that for a bird to change direction in a steady-state turn (i.e. continuous lift production and non-flapping wings) it requires an initiating force asymmetry, followed by an arresting force asymmetry. Disparate forces produced by the wings cause the bird to roll into a bank (wings making an angle Φ to the horizontal), redirecting lift towards the desired direction of flight. Then, the initial force asymmetry must be reversed to halt the rolling momentum. Now, the bird turns at a constant rate, and no further force asymmetry is needed to maintain the bank once it has been established. We express the balanced forces in the vertical-transversal plane acting on a bird that initiates a gambit by pronation/supination of the wings, thus engaging in a pure-rotation bank, and demonstrate that the turning capabilities are dominated by body mass. We take equation 2 from Hedenström & Rosén (2001) as a starting point. This shows how to compute turning-radius, r, of a bird circling with azimuthal velocity v, from the radial forces acting on the bird. These are the inwards directed component $L\sin\Phi$ of the lift force L which balances the outward directed centrifugal force Mv^2/r, where M denotes body mass. This leads to

$$r = Mv^2/L\sin\Phi.$$

In the vertical direction, the force of gravity, Mg (g denoting the acceleration of gravity), is balanced by the upward directed component of the lift force:

$$Mg = L\cos\Phi.$$

Using the trigonometric relation $\cos^2\Phi + \sin^2\Phi = 1$, this yields

$$M^2g^2/L^2 + M^2v^4/L^2r^2 = 1,$$

Solving for the radius r yields:

$$r = v^2 (L^2M^{-2} - g^2)^{-1/2}.$$

Now, the lift force induced by flow around the wing is itself proportional to the squared velocity

$$L = 1/2\ \rho v^2 SC_l\ ,$$

where ρ = density of air at sea level = 1.23 kg/m^3, S = wing surface area and C_l = lift coefficient = 0.5 (Hedenström & Rosén 2001). Defining proportionality constant α [kg.m^{-1}]

$$\alpha = \rho\ S\ C_l/2,$$

we have

$$L = \alpha v^2.$$

Inserting this into the expression for the radius, we find

$$r = v^2/ (\alpha^2v^4/ M^2 - g^2)^{1/2}.$$

Therefore, for large velocities,

$$\lim_{v\to\infty} r(v) = \lim_{v\to\infty} v^2/ (\alpha^2v^4/ M^2 - g^2)^{1/2} = M/\alpha,$$

the radius approaches its minimum, $r_{min} = M/\alpha$, which clearly decreases with decreasing body mass M. We will illustrate these calculations when discussing our experiments.

Howland (1974) explains that at some high velocity an additional effect must set in, namely that of a limit to the centrifugal acceleration that a bird can withstand. Given that the animal is moving sufficiently fast that this limit is reached, then for every increase in velocity it must also increase its turning-radius in proportion to the square of its velocity in order to stay within the limit of constant centrifugal acceleration (in general the lift of a wing will be proportional to the square of the velocity at which the bird moves). Above a certain level, speed will be lost at the expense of turning-radius. This constraint can be counteracted by body mass decrease.

In conclusion, we expect nearshore foragers to be generally speed-based escapers that respond to increased predation pressure by pectoral muscle mass increase. Farshore foragers are expected to be agility-based escapers that respond to increased predation threat by a decrease in general body mass.

Based on a comparative literature study among passerines, Swaddle and Lockwood (1998) concluded that species with relatively rounded wingtips and relatively short femora compared with tarsi, were at a lower predation risk than species with more pointed wingtips and relatively longer femora. Burns & Ydenberg (2002) proposed that habitat related escape tactics in two closely related Calidrid species may have contributed to differences in both wing and hind limb morphologies between the two species. Yet, they rightfully acknowledge that wing shape likely evolved under multiple, and possibly conflicting, selection pressures, related to predation, migration, reproduction (display flight) and foraging. For instance, it has been argued that the demands of migration may have set the stage for the high aspect ratio wings of many long-distance migrants, while special foraging techniques may have contributed to differences in wing shapes between coursing and hawking insectivorous bird species (Warrick 1998). Thus, differences in wing shape due to escape tactics may be subtle. We expect that speed-based escapers should have relatively low aspect ratio, or relatively rounded, wings, whereas socially-coordinated escapers are expected to have relatively high aspect ratio or relatively pointed wings. Finally, molt gaps decrease wing surface thus increasing wing loading. As this will decrease escape flight performance thereby increasing vulnerability to predation, compensatory measures are expected to be similarly associated to the birds' ecologies.

A FIRST TEST OF THE PREDICTIONS

Small flocks of birds may be randomly exposed to simulated predator attacks, for instance by gliding a raptor model overhead. Body mass (using a balance) and pectoral muscle mass (using ultrasonography - Dietz *et al.* 1999a) may be measured before and after the experiment, limiting disturbance effects by the researcher as much as possible. To examine possible relationships between escape tactic and responses in pectoral muscle and body mass, such experiments could be performed with different, similar-sized, species, with different ecologies (nearshore/farshore foragers). There are a number of shorebird species that typically forage in nearshore areas, such as rocky shores and sandy beaches (e.g. Whimbrel *Numenius phaeopus*, Black Turnstone *Arenaria melanocephala*, Ruddy Turnstone *Arenaria interprès*, Purple Sandpiper *Calidris maritima*, Sanderling *Calidris alba*, Rock Sandpiper *Calidris ptilocnemis*, Surfbird *Aphrizia virgata*, Common Sandpiper *Actitis hypoleucos*, Spotted Sandpiper *Actitis macularia*, and a number of *Charadrius* plovers). Others are more typical of open areas, such as Red Knot *Calidris canutus*, Dunlin C*alidris alpina*, and Western Sandpiper *Calidris mauri*.

We performed such an experiment in the indoor Experimental Shorebird Facility at the Royal Netherlands Institute for Sea Research with Red Knots (a farshore forager species) and compared this to a similar experiment (same facility, similar set-up) with Ruddy Turnstones (a nearshore forager species) (van den Hout *et al.* 2006). We examined body mass and pectoral muscle mass changes in response to exposure to a model predator. We only describe the methods of the Red Knot experiment, referring to Van den Hout *et al.* (2006) for the turnstone experiment.

METHODS

Using mistnets, fifty Red Knots were caught on Richel (53°16'57" N, 05°23'82" E) and on Simonszand (53°29'28"N 06°24'19"E), in the Wadden Sea, The Netherlands, on 8 August and 3 September 2005, respectively. We selected adults of the *islandica* subspecies (e.g. Nebel *et al.* 2000, Piersma 2007). The birds were housed in aviaries at the Royal Netherlands Institute for Sea Research (NIOZ) in four flocks of 12 to 13 birds. The aviaries measured 3.85 m by 1.85 m and were 2.40 m high. Air temperature and photoperiod were determined by the ambient outdoor conditions. Each group of experimental birds was set free in the Mokbaai, Wadden Sea (53°00'37"N, 04°45'11"E) immediately after the experiments. From the beginning of their time in captivity, the birds were fed *ad libitum* with 2-4 mm Mudsnails (*Hydrobia ulvae*), which had been collected from the Wadden Sea. Mudsnails were stored frozen and thawed immediately before use (Vézina *et al.* 2006).

Some of these birds were molting their primaries, and we were aware that this might confound our results. Therefore, to enable statistical control for molt later on, birds were scored for growth of primaries (0 = old, 1 = shed, 2 = quarter grown, 3 = half grown, 4 = three quarters grown, and 5 = fully grown feather – Ginn and Melville 1983). To estimate the size of the gap in the wing caused by missing or growing feathers, we used the measurement of wing raggedness, which corresponds to the molt score such that the sum of the molt score and the raggedness score is five for each new or growing feather. As neither an old nor a fully-grown feather causes a gap, both have a raggedness score of zero (Bensch & Grahn 1993). Although this measure does not account for the position of the gap in the wing (Hedenström & Sunada 1999), it is nonetheless adequate for exploring possible molt effects within individuals.

The experiments took place from 21 August through 28 November 2005 in an indoor mudflat facility (7 × 7 × 3.5 m high; see figure in Mathot *et al.* 2009). During the experiments a constant light-dark cycle was implemented (lights on from 6h00 to 21h00), with 'moonlight' illumination being provided during the dark phase. We carried out eight trials, each with a flock of six birds which were randomly selected from each of the four outdoor flocks. Each trial consisted of a two-day habituation period, followed by a five-day control and a five-day experimental period. This time frame was used because it is expected to be sufficiently long to allow detectable changes in pectoral muscle mass and total body mass (Dietz *et al.* 1999b, Piersma *et al.* 1999, van den Hout *et al.* 2006). The order of experimental and control periods was determined at random for each flock, with flocks receiving the experimental period first and last in four trials each.

During the trials two event types were used to simulate predation danger. The first consisted of a gliding Sparrowhawk *Accipiter nisus*, L. model accompanied by digital playback of wader alarm calls. This event lasted about 5 s. The stuffed model glided across one side of the indoor mudflat, passing over the food tray (see Mathot *et al.* 2009). The second event type involved presenting a model of a perched Sparrowhawk supplied with a built-in electromotor which allowed head movement. The perched Sparrowhawk was hidden behind a black curtain except during 'perching' events, when the curtain was lifted and the perched model was rolled into the mudflat arena, for 1 min, approximately 0.5 m above the mudflat surface. During the experimental periods, 'gliding' and 'perching' events were carried out once each day at unpredictable times between 9h30 and 17h00 with the constraint that events did not occur within 90 min of each other in order to allow sufficient time for focal observations between events. Behavioral responses to the raptor threats in this experiment, including details of observational methods, were discussed in a separate paper (Mathot *et al.* 2009).

In the previous experiment (van den Hout *et al.* 2006), it was established that shorebirds are able to distinguish predators from non-threatening disturbances. Having shown this and trying to avoid any other disturbance of the Red Knots in the experimental arena, we did not provide a non-threatening disturbance as control. During all phases of the trials (i.e. habituation, control and experiment), at 18h00 the mudflat was briefly (10-30 min) flooded with sea water to help cleanse the sandy substrate. During this time, the birds could rest on an elevated roosting platform (Mathot *et al.* 2009). Food was also replaced at this time. Trays of freshly thawed Mudsnails were provided in sufficient quantity to allow *ad libitum* feeding for the subsequent 24h.

Morphological changes were measured as the differences between the onset and the end of each control and treatment period. Body mass (BM) was measured to the nearest 0.1 g on a balance (Sartorius, type 3862). Pectoral muscle size (muscle thickness, to the nearest 0.1 mm) was measured by PJH, and in the last two trials by Anne Dekinga (AD), using an ultrasound apparatus with a 7.5 MHz linear probe (Pie 200, Pie Medical Benelux BV, Maastricht, The Netherlands; for further details, see Dietz *et al.* 1999a). As PJH was aware of the treatment that birds were exposed to, in each session of ultrasound measurements three dummy birds were randomly included to test for observer bias. There was no such observer bias as treatment and control values did not differ for these dummy birds (GLM, $F_{1,24} = 0.139$, $P = 0.713$). The measurements were otherwise 'blind' in the sense that no readings were made by the observer, but only ultrasound pictures that were subsequently interpreted by a second observer. Ultrasound measurements showed a repeatability of 0.83 for PJH and 0.80 for AD (Lessells & Boag 1987, Dietz *et al.* 1999a). We computed pectoral muscle mass (PMM) (g) from muscle thickness (MT) (mm) using the predictive equations derived from a calibration exercise on Red Knot carcasses (these birds died as a result of catching accidents on the Banc d'Arguin, except for three birds that collided with a light house in the German Wadden Sea): for the measurements taken by PH: $PMM = -0.35 + 0.40MT$ ($R^2 = 0.24$, $N = 16$, $P = 0.030$); for AD: $PMM = -9.58 + 0.28MT$ ($R^2 = 0.40$, $N = 18$, $P = 0.003$). During the first experiment (which started off with a control treatment), no pectoral muscle data were obtained because of instrument failure. This limited the comparisons involving pectoral muscle thickness to seven trials.

Data were analyzed using linear mixed effects models (LME's) from the package 'nlme' in R (v. 2.6.1). LME's provide estimates of the influence of fixed effects on the mean and random effects on the variance, accounting for the non-independence of errors resulting from the repeated measures on individuals. Statistically, trials are comprised of the successive treatments each carried out with a different 'group'. Using repeated measures, each individual served as its own control. To remove body size related variation among individual birds, all mass variables were standardized, by dividing them by the values at the start of the trial. We tested for differences in body mass and pectoral muscle thickness between the predator treatment and the control, using models with treatment, treatment order (control or predator first) and the interaction of treatment and treatment order as fixed effects, and individual within group within order as a random effect. As treatment order could not be tested as both a fixed factor and as part of a nested complex of random factors (treatment order/group/individual), we compounded order and group into unique combinations, leaving only two nesting levels (~1|treatment order&group/individual).

Although alternating 'treatment order' would serve to control for seasonal effects, including molt, we chose to include raggedness of the wing as a covariate in the analysis (in the LME package of R, the covariate, raggedness, is used in the model statement, thus considered a fixed effect) to control for possible effects of molt on the response variables of interest (body mass and pectoral muscle thickness). Midpoint measurements of primary molt would create too much disturbance to the experimental birds, and consequently, we took molt scores immediately after each experiment. However, as during the first three trials primary molt data were taken immediately before the experiment, we interpolated these values to values expected at the end of a trial, by calculating the speed of growth for each primary. These calculations were based on primary molt patterns estimated from weekly measures of 55 Red Knots kept in the outdoor aviaries at our institute in autumn 2001 and 2002.

Assumptions of normality and homoscedasticity were verified by visual inspection of probability plots. Raggedness values were square root + 0.5 transformed to meet requirements of normality (Zar 1999). We ranked all possible models using the Akaike Information Criterion (AIC) (Akaike 1974), and selected the highest ranked model (with lowest AIC) as our final model.

EXPERIMENTAL RESULTS

Upon the appearance of both the gliding and the perching Sparrowhawk, Red Knots always took flight, and remained airborne for 34.7 ± 1.3 s (mean ± s.e.m., N = 240) after hawk flight events and 28.2 ± 1.3 s (mean ± s.e.m., N = 240) after hawk perching events.

The minimally adequate model for changes in both body mass and pectoral muscle mass included treatment and raggedness as fixed effects (Table 9.1). Exposure to the raptor models resulted in average body mass reduction of 2.6% ($P < 0.001$; Table 9.2A). When the control preceded the predator treatment, body mass increased with an average 4.8% (from 122.1 g to 128.0 g) during the five-day control phase of the experiment and decreased by 2.3% (from 128.0 g to 125.1 g) during the subsequent five-day predator phase. In contrast, when the raptor models were presented first, despite a tendency for body mass increase during the entire experimental period (see values with respect to baseline in Figure 9.2), body mass at

Table 9.1 Model selection for tests of responses of body mass (BM) and pectoral muscle thickness (PMT) to raptor exposure. Treat=treatment, order=treatment order, rag= raggedness. In the LME package of R the covariate raggedness is used as a fixed factor. The minimal model, with lowest AIC value, was chosen for both dependent variables.

Model (random=~1|order&group/individual) Dependent variable:	BM		PMT	
	Rank	AIC	Rank	AIC
Treat + order + rag + treat*order + treat*rag + order*rag + treat*order*rag	8	–289	8	–196
Treat + order + rag + treat*order + treat*rag + order*rag	7	–295	7	–202
Treat + order + rag + treat*order + treat*rag	6	–303	6	–209
Treat + order + rag + treat*order + order*rag	5	–305	5	–209
Treat + order + rag + treat*rag	4	–313	4	–217
Treat + order + rag + treat*order	3	–314	3	–217
Treat + order + rag	2	–323	2	–225
Treat + rag	1	–330	1	–232

the end of the raptor treatment was not different from starting mass, but subsequently increased during the control phase by 2.7% (from 126.7 g to 130.0 g; Figure 9.2A). Unlike body mass, pectoral muscle size was not affected by the raptor model intrusions ($P = 0.562$; Table 9.2A; Figure 9.2B).

In the model testing for the effects of treatment on body mass, the random factor 'group', compounded with 'order' (see Methods) was responsible for 56% of the random error. This was around 23% for 'individual' nested within 'group&order' (Table 9.2B). In the model addressing pectoral muscle as the response variable, these values were 33% and 49% respectively (Table 9.2B). Molt (measured in raggedness values) tended to affect body mass ($P = 0.090$; Table 9.2A), but this effect was not significant; neither was the interaction term treatment*raggedness ($P = 0.950$). Raggedness, however, did influence pectoral muscle thickness ($P < 0.001$; Table 9.2A). Yet, neither treatment ($P = 0.562$; Table 9.2A), nor the interaction term treatment*raggedness significantly affected pectoral muscle thickness ($P = 0.318$). Analysis of the interaction terms indicate that differences at individual or group level in primary molt phase did not confound the effects of predator exposure on either body mass or pectoral muscle thickness.

Table 9.2 A. LME test results for effects on values of body mass and pectoral muscle size. The results for pectoral muscle size were based on trials 2-8 only, due to instrument failure during the first trial. B. Random effects. Note that Group and Order were compounded to one random factor (see Methods). Note that R (nlme package for mixed models) treats the covariate raggedness as a fixed effect.

A Fixed effects	effect size	CI	df	t	*P*
Dependent variable: body mass					
Treatment	–0.026	–0.036 – –0.015	1	–4.962	<0.001
Raggedness	–0.010	–0.022 – 0.002	1	–1.735	0.090
Dependent variable: pectoral muscle size					
Treatment	–0.005	–0.023 – 0.013	1	–0.585	0.562
Raggedness	0.039	0.021 – 0.058	1	4.256	<0.001

B Random effects	St dev	relative contribution to variance (%)
Dependent variable: body mass		
Group&Order	0.0398	55.9
Group&Order/Individual (intercept)	0.0247	21.5
Group&Order/Individual (residual)	0.0254	22.7
Dependent variable: pectoral muscle size		
Group&Order	0.0334	32.6
Group&Order/Individual (intercept)	0.0411	17.9
Group&Order/Individual (residual)	0.0248	49.4

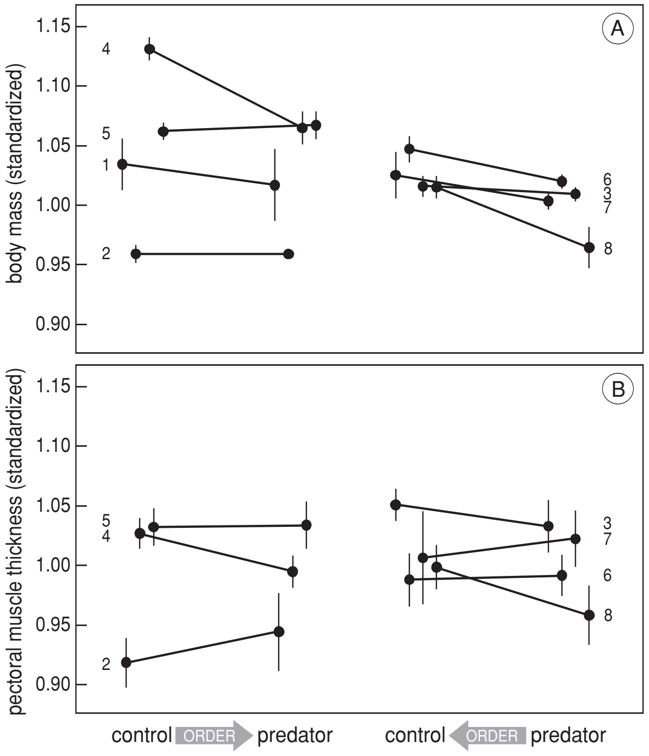

Figure 9.2 Changes in body mass (panel A) and pectoral muscle thickness (panel B) due to simulated raptor attacks compared with control treatment for each of the experimental trials separately. Variance around the means is shown by error bars (± 1 SE). The values are averages of six birds, and were standardized to the values at the start of the trial. Treatment orders (predator or control first) are depicted explicitly. Trial 1 for pectoral muscle is missing due to instrument failure.

DISCUSSION

We use aerodynamic theory to develop predictions for the morphological response to predation danger of different classes of bird species, based on differences in their ecologies. Escape speed should be critical for nearshore species owing to the short predator detection distances, which should favor higher pectoral muscle mass. In contrast, farshore species should favor maneuverability, and decrease mass in response to predation danger. A comparison of the Red Knot experiments with an earlier experiment with Ruddy Turnstones (van den Hout *et al.* 2006) provide preliminary evidence for species specific morphological responses to predation which match the differential ecologies of those species.

Following five days of exposure to simulated predator events, Red Knots decreased their overall body mass, while pectoral muscle mass remained unchanged. Ruddy Turnstones showed a different morphological response than Red Knots, increasing pectoral muscle mass without a significant increase in body mass (fat-free mass did not change either). Instant responses to predator exposure also differed between these species: while Red Knots as a rule immediately flew off, Ruddy Turnstones generally responded by crouching and freezing.

The differences between Red Knots and Ruddy Turnstones in morphological response to predation are consistent with the predictions outlined earlier based on differences in their ecologies and related escape tactics. Ruddy Turnstones feed in shoreline habitats, mainly foraging in small and scattered groups (Metcalfe 1986). They occur on beach-cast wrack and near the cover provided by rocks and other habitat structures (Cramp *et al.* 1983, Metcalfe 1984, Fuller 2003). Here they are particularly vulnerable to surprise attacks by raptors such as Sparrowhawks and large falcons, *Falco* species (Metcalfe 1984, van den Hout *et al.* 2008). When attacked by a raptor, Ruddy Turnstones have the option to freeze in the cryptic environment of crevices. However, if capture is imminent (Ydenberg and Dill 1986), they rely on a speed-based escape, often towards an open water surface (Whitfield *et al.* 1988), or into saltmarsh vegetation (Lima 1993). In view of the close range at which these species generally detect the predator, the early stage of escape is decisive for survival. This requires fast take-off and acceleration, that is, a speed-based escape. Increasing power output by boosting pectoral muscle best matches such an escape scenario.

In contrast, Red Knots tend to forage in large flocks in very open mudflat habitats avoiding topographical structures that would allow raptors to attack by surprise (Piersma *et al.* 1993, van den Hout *et al.* 2008). Other than Ruddy Turnstones which are often ambushed by raptors, through the ‘many eyes’ available for scanning an unobstructed environment, Red Knots, as a rule, have more time to prepare themselves for an escape response. As soon as an aerial attacker is detected, Red Knots take flight as a flock and perform coordinated aerial escape flight maneuvers (Lima 1993; van den Hout *et al.* 2008). As predicted, rather than responding to predation danger by increasing the size of their pectoral muscles as in Ruddy Turnstones (van den Hout *et al.* 2006), Red Knots responded with a decrease in body mass (though not at the expense of pectoral muscle mass) in favor of turning maneuverability. Applying the earlier mathematical calculations, we visualized the results of the Red Knot experiments in Figure 9.3. This figure shows that the benefit for Red Knots is twofold. First, the body mass reduction directly reduces inertia, and thus turning-radius (Origin to position A); second, by decreasing body mass, while keeping pectoral muscle size unchanged, Red Knots increase power output, and thus velocity, which leads to a further reduction in the turning-radius (from A to B). Instead, the Ruddy Turnstones increase pectoral muscle mass (van den Hout *et al.* 2006), moving them away from the y-axis along a turnstone-specific isocline, which mainly results in higher speed.

The benefit of body mass decrease for overall flight capacity can also be demonstrated using the aerodynamic considerations for flight performance (based on wind tunnel studies) in Dietz *et al.* (2007). They predicted that for flight performance to

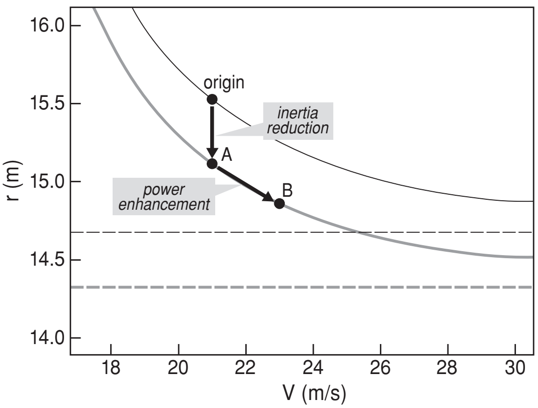

Figure 9.3 Isoclines reflecting turning-radii as a function of velocity, as predicted by the model of Hedenström and Rosèn (2001), shown for the average of both orders (raptor-control and vice versa) in the experiment. This returns 129.0 g for control (thin black curve) and 125.9 g for the predator treatment (thick grey curve). Predicted minimum turning-radii for birds in the raptor treatment and the control are determined by the asymptotes in the figure, yielding 14.67 m (thin dashed black line) and 14.32 m (thick dashed grey line) respectively. Calculations of the asymptotic values were given earlier in the text. The twofold benefit of a decrease in body mass is shown qualitatively: Origin to position A denotes the decrease in turning-radius due to decreased body mass; A to B shows the additional decrease in turning-radius due to a relative increase in power output (see text). The Ruddy Turnstones in Van den Hout *et al.* (2006) would move along a turnstone-specific isocline, towards higher speed, with a minor decrease in turning-radius (equivalent to the trajectory from A to B in this figure).

remain constant, pectoral muscle mass should scale allometrically with body mass to the power 1.25. In our experiment, in the control phase, Red Knots obtained an average body mass of 129.0 g and a pectoral muscle mass of 29.9 g. The birds that decreased body mass to 126.0 g after the raptor scares obtained a pectoral muscle of 29.7 g, 2.4% higher than the 29.0 g that would follow from this allometric relationship. Thus, Red Knots, following exposure to predators, as well as gaining greater maneuverability during the predator phase of the experiment, also achieved increased flight capacity (PMM/BM$^{1.25}$; Figure 9.4).

Our experiment was not designed to examine the effects of primary molt (raggedness) on mass components. Instead, we were confronted with some molting birds as a result of logistical (seasonal) constraints. Still, the examination of molt as a covariate yielded an interesting insight. There are not many studies on the effect of primary molt on pectoral muscle and most address waterfowl with respect to their virtually flightless period (Piersma 1988, Fox & Kahlert 2005), but see Lind & Jakobsson 2001). We now see that molt correlates with a significantly larger pectoral muscle size in a shorebird fully capable of flight. However, in our experiment the correlation between molt and pectoral muscle size was independent of the effects of predation threat on body mass. Furthermore, there is no evidence that the absence of effect on pectoral muscle size is due to molt effects (Table 9.1).

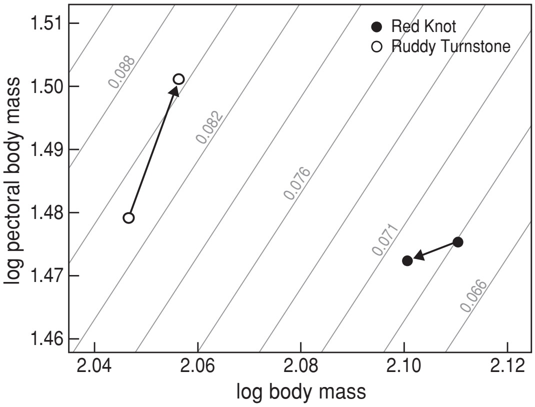

Figure 9.4 Phase space with lines for equal flight capacity (PMM/BM$^{1.25}$) (Dietz *et al*. 2007), for Ruddy Turnstones (Van den Hout *et al*. 2006) and Red Knots (this study), showing that in response to raptor model intrusions both species increase flight capacity, Red Knots by decreasing body mass and Ruddy Turnstones by increasing pectoral muscle size (all data were log-transformed). Vector directions are based on average values. Small changes in body mass (for Ruddy Turnstone), and pectoral muscle size (for Red Knot), although insignificant, contribute to the vector directions.

As predicted, the difference in escape behavior of Red Knots and Ruddy Turnstones is not only correlated with their different ecologies, but is also associated with differences in wing morphology. Although both Red Knots and Ruddy Turnstones are long-distance migrants with the predicted long slender wings (Alerstam & Lindström 1990, Marchetti *et al.* 1995), the aspect ratio of Ruddy Turnstone wings is 10% lower (7.9 ± 0.11, N = 29) than of Red Knot wings (8.7 ± 0.05, N = 65; t = –5.85, df = 39.6, $P < 0.001$), indicating that Ruddy Turnstones have relatively shorter and broader wings than Red Knots.

For Red Knots, maintaining coordinated movements with the rest of the flock is critical for any given individual in order to avoid being singled out in a one-to-one chase with the raptor (Caro 2005). This means that even subtle differences in maneuverability performance would translate into large differences in the probability of being killed. In view of the risks of being less agile than other flock mates, we expect selection for prey to have the ability to monitor the state of conspecifics in the same and different groups so that they assess relative vulnerability and respond appropriately (Cresswell & Quinn 2004). In such a game-theoretic scenario, for birds facing a trade-off between safety and energy even a subtle sacrifice in energy stores could thus have a significant payoff in terms of survival. However, the present experiment does not tell us whether in nature a period of more than five days of elevated danger would yield larger effects than we detected.

Previous observations have shown that pectoral muscle mass rapidly tracks changes in body mass in Red Knots (Lindström *et al.* 2000). Thus, if the morphological changes observed in Red Knots following exposure to predators were merely a passive consequence of the increased flying and reduced feeding rates following exposure to predators, we would expect the pectoral muscle mass to decrease. Similarly, it seems unlikely that, in the Red Knots, flight activity due to the raptor disturbance caused pectoralis hypertrophy and simultaneous mass loss. Swaddle and Biewener (2000) showed that, as opposed to the muscle use-disuse hypertrophy-atrophy hypothesis (Marsh 1984, Gaunt *et al.* 1990), pectoral muscle mass in starlings induced to perform more take-off flights actually decreased as a result of exercise. In contrast, the Red Knots in our experiment, whilst decreasing body mass, apparently defended pectoral muscle mass, thus increasing their flight output, likely as an anti-predation measure rather than responding to workload (see also Witter *et al.* 1994). Similarly, in the experiment on Ruddy Turnstones (van den Hout *et al.* 2006), if changes in mass of body components were simply a consequence of behavioral changes induced by exposure to predators, changes in lean mass and pectoral muscle mass should have been correlated with one another. Instead, in Ruddy Turnstones the increase of pectoral muscle mass was decoupled from lean mass. We suggest that the turnstones' reluctance to fly upon raptor intrusions (van den Hout *et al.* 2006), which in nature would be enabled by their cryptic environment, additionally serves to conserve muscle power in the case that escape becomes inevitable. The fact that Ruddy Turnstones, though not flying, increased pectoral muscle size, whereas Red Knots, while engaging in escape flights, did not (at least not in absolute sense), also hints to controls other than 'use-disuse' mechanisms of these body components (Dietz *et al.* 1999b, Portugal *et al.* 2009).

Flock was included as a random effect in our model because it was not a variable of interest for the hypothesis we were testing. However, our data clearly show strong differences between groups in their morphological response to predation. Although we could develop hypotheses for why groups differed (for example: differences in group composition such as sex, dominance, or personality profiles), this was not the focus of the current study. Despite large variation between groups, we still detect a significant effect of treatment on changes in body mass, which suggests that treatment (predator/control) is an important factor mediating changes in body mass.

The fact that several experimental studies (as reviewed in Caro 2005) report higher threshold values for body mass to impair flight velocity or angle than the 2.6% body mass change reported in this study (Table 9.1), does not refute our conclusions for at least two reasons. First, rather than body mass, or even wing loading, alone, the ratio of pectoral muscle to body mass reflects flight capacity (Lindström *et al.* 2000, Dietz *et al.* 2007). The impaired flight performance in the experiments testing flight performance as a function of wing loading may well have been caused by minor changes in this ratio, instead of body mass increase alone. In fact, compensatory pectoral muscle mass increase may explain why other studies failed to find an effect of a moderate body mass increase (Kullberg *et al.*, 1998, van der Veen & Lindström 2000), even though effects were evident with high fuel loads (Kullberg *et al.* 1996, Dietz *et al.* 2007). Second, most studies measured only one or few maneuvers, which may come close to the natural situation of a passerine escaping into nearby cover. Yet, this does not compare to the persistent maneuvering of shorebirds escaping in a flock (Lima 1993, Rudebeck 1950-1951). In fact, just as human athletes experience in acrobatics (Fox *et al.*, 2008), e.g. in a balance beam routine, in birds minor agility 'deficiencies' may add up to a fatal error in a sequence of maneuvers.

PROPOSING A RESEARCH PORTFOLIO

This study provides preliminary support for the hypotheses developed in the introduction. However, further studies are required. Although use of ultrasound equipment for measuring pectoral muscles may be logistically unfeasible for many researchers, dental alginate exists as a cost effect alternative for obtaining coarse estimates of pectoral muscle size (Selman & Houston 1996).

To test whether changes in body composition as detected in experiments are biologically meaningful, additional experiments may be needed, in which flight performance parameters, such as linear acceleration and turning speed and radius are coupled to differences in body mass and pectoral muscle mass respectively. Specific methods may depend on the size of the experimental bird species. To our knowledge, in all flight performance studies, birds of which flight performance was tested accelerated from a stationary position (Swaddle *et al.* 1999, Lind 2001, Burns & Ydenberg 2002), thus basically addressing a speed-based escape mode. Likewise, detailed studies of maneuverability typically involve maneuvering at relatively low speed (Warrick 1998, Warrick *et al.* 1998). To our knowledge, high velocity maneuvers have never been studied in detail due to logistical constraints. Even more logistically challenging, but necessary for a full understanding of the proposed relationship between escape tactic and adaptive changes in body composition due to raptor threat, would be to measure flight parameters of birds involved in socially-coordinated escape flight (for inspiration, see Potts 1984).

Other tractable systems, in addition to nearshore and farshore shorebird foragers, for testing this hypothesis include passerine taxa. The Emberizinae are a subfamily of the Passeriformes which are notable for a high diversity of escape tactics (Lima 1993). For instance, within Fringillidae, a diversity of escape tactic from herbaceous- and woody-vegetation-dependent escape tactics are represented (Lindström 1989). Several arboreal, socially feeding fringillids (Crossbills *Loxia* species, Pine Siskins *Carduelis pinus*, Evening Grosbeaks *Coccothraustes vespertinus*) employ highly coordinated flight and flushing behavior. This may be related to the use of more exposed feeding habitat due to weak familiarity with the location and nature of protective cover of these nomadic species (Lima 1993). We hope that this study will initiate a portfolio of novel studies in phenotypic flexibility and predation in the context of a species' ecology.

ACKNOWLEDGEMENTS

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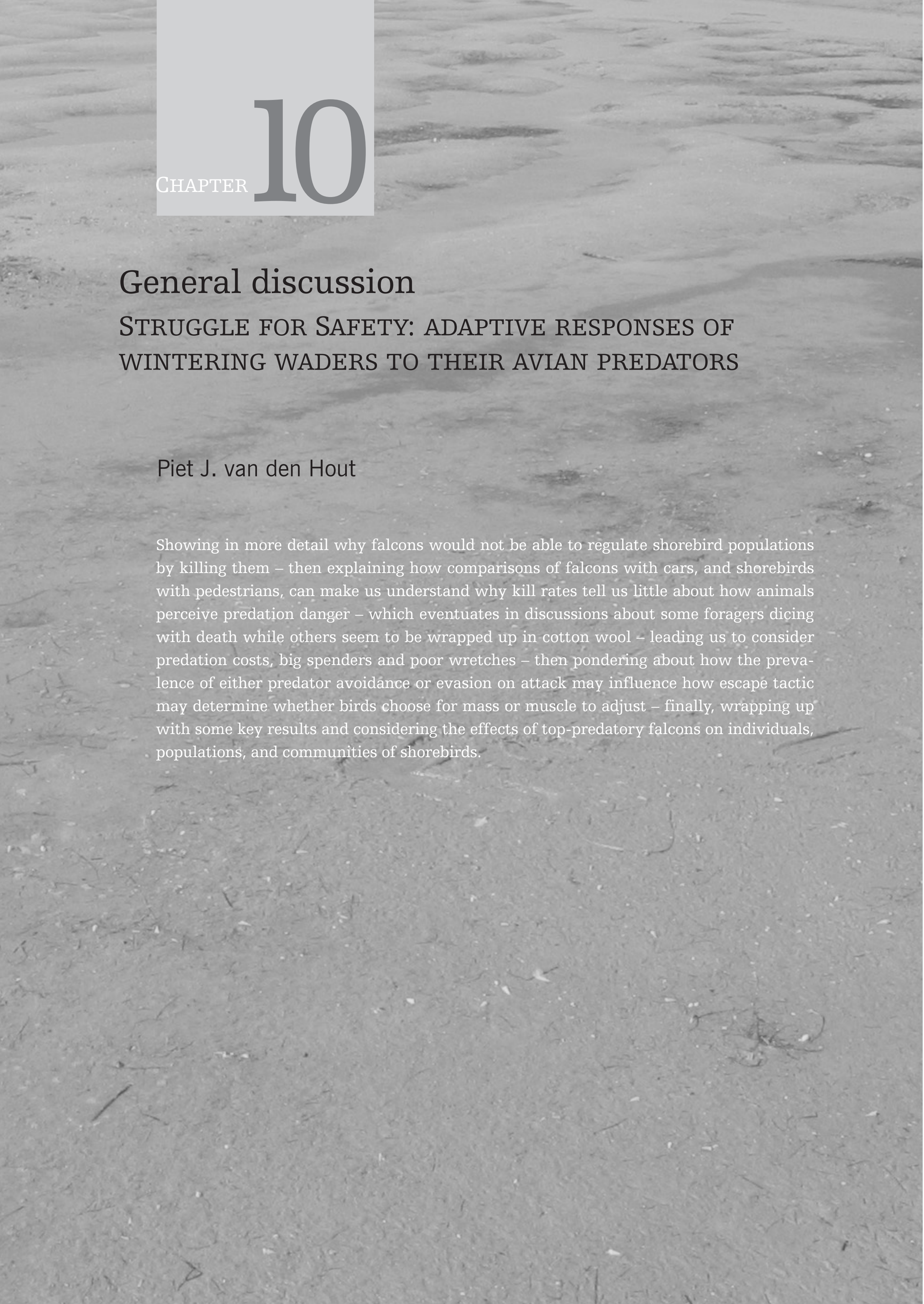
PART IV

GENERAL DISCUSSION


Carl Zeiss



CHAPTER 10

General discussion

STRUGGLE FOR SAFETY: ADAPTIVE RESPONSES OF WINTERING WADERS TO THEIR AVIAN PREDATORS

Piet J. van den Hout

Showing in more detail why falcons would not be able to regulate shorebird populations by killing them – then explaining how comparisons of falcons with cars, and shorebirds with pedestrians, can make us understand why kill rates tell us little about how animals perceive predation danger – which eventuates in discussions about some foragers dicing with death while others seem to be wrapped up in cotton wool – leading us to consider predation costs, big spenders and poor wretches – then pondering about how the prevalence of either predator avoidance or evasion on attack may influence how escape tactic may determine whether birds choose for mass or muscle to adjust – finally, wrapping up with some key results and considering the effects of top-predatory falcons on individuals, populations, and communities of shorebirds.

PROLOGUE

War Memorial Day, the 4th of May 2010, Amsterdam, The Netherlands. Ceremonies in the presence of the Royal Family are taking place in all earnestness and contemplation. Suddenly crowds of people break apart and scatter in all directions while running over crush barriers and fellow-citizens in a panic response to an expanding wave of vague alarms that were elicited by a harmless scream of a lunatic. Like a herd of Zebra's startled by a noise which could have been a Lion approaching; or a placidly foraging shorebird flock, suddenly bursting apart after an alarm call emitted by a hot-tempered Whimbrel…

THE ROLE OF TOP-PREDATORS IN ECOSYSTEMS

The event just described poignantly indicates that fear for attack and depredation is deeply engraved in the system of potential prey. In this thesis, shorebird prey and their most-feared predators, falcons, were the focus of attention. Falcons are considered *top*-predators as they represent the apex of the food chain. Over the last decades there has been a lot of debate about the role of top-predators in ecosystems: are they a necessary component of the ecosystem, holding populations in check and promoting biodiversity, or are they a nuisance factor in community dynamics because the systems are controlled in a bottom-up direction (Sih *et al.* 1985, Ale & Whelan 2008)? Although this dispute has largely been settled – with an abundance of evidence showing that predators can have enormous influences on the structure and the dynamics of ecological populations and communities (Sih *et al.* 1985, Chase 1987, Stolzenberg 2008) – the attention has largely been concentrated on the large carnivores such as big cats, wolves, Grizzlies and sharks (Ale & Whelan 2008, Stolzenberg 2008). Less attention has been given to Peregrine Falcons *Falco peregrinus* and other avian predators (but see Thirgood *et al.* 2000, 2002). Therefore, although the main aim of this thesis is to get a better understanding of shorebird foraging in the face of predators, the results may also give us better insights in the structuring roles of these top-predators in ecosystems.

WHY FALCONS MAY LIMIT, BUT SELDOM REGULATE SHOREBIRD PREY

Predators can delimit prey numbers in either a regulatory (density-dependent), or a non-regulatory (density-independent) way (Solomon 1949, Newton 1998). If predators regulate their prey in a density-dependent manner, this means that the proportion of prey that are killed increases with increasing density of prey, so that predators check the rate of increase as prey numbers rise and restrain the decrease as prey numbers fall (Newton 1998).

The (generalized) functional response is the relationship that specifies the rate at which an average predator (consumer) consumes a given resource as a function of the density of that resource and the density of consumers (Holling 1966, Abrams 1987). Through the built-up of energy and nutrients for reproduction, ultimately leading to higher predator numbers, the functional response may directly affect the numerical response, that is, the dependence of predator density on prey density (Newton 1998, Nielsen 1999).

The most common functional responses that we find in nature are types II en III (Holling 1959a,b, 1966, Van der Meer & Ens 1997, Jeschke *et al.* 2002). Constraints upon predation rates differ for low and high prey densities. Decreasing predation rates at high densities has usually been attributed to either handling time or satiation, but Jeschke *et al.* (2002) note that digestion does not necessarily prevent a predator from further searching or handling (see Fig. 10.1).

Predation limitation at low densities are commonly attributed to low searching efficiencies (Holling 1959b, Curio 1976, Van der Meer & Ens 1997, Jeschke *et al.* 2002), for instance because a predator may need reinforcement of prey encounters to develop a search image, or because at low densities most prey will hide in refugia (which would all be occupied at higher prey densities). The predation cycle involves a numbers of stages (Fig. 10.1). When a searching predator encounters prey (β in Fig. 10.1) it may or may not detect it (δ in Fig. 10.1). When it detects the prey it may or may not attack (α in Fig. 10.1). Most functional response models assume that whenever a searching predator encounters and detects a prey, it will attack, i.e. $\alpha = 1$ in Fig. 10.1 (reviewed in Holling 1966, Jeschke *et al.* 2002). However, this assumption

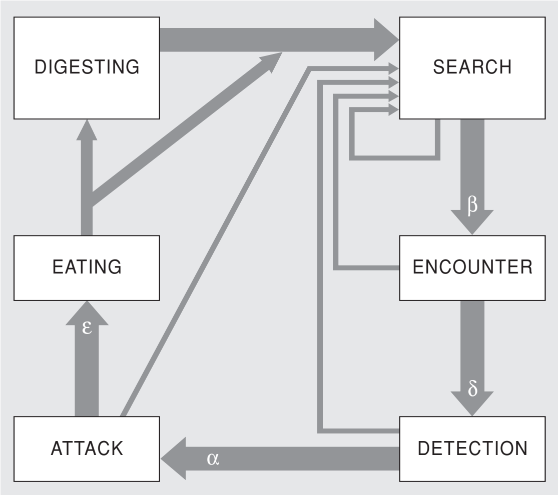


Figure 10.1 The predation cycle, divided into five mutually exclusive and sequential states: search, encounter, detection, attack, and eating (digestion can be partly combined with searching, so these are not mutually exclusive states). The probability of encounter is denoted by β, while δ stands for the probability of detection. The probability of attack (α) and the probability of successful attack (ε) largely determine the accelerating part in the type III response that is depicted in Fig. 10.2A (see text for further explanation). Diagram adapted from Jeschke *et al.* (2002).

does not seem realistic for predator-prey relationships in which attack efficiency (ε in Fig. 10.1) depends largely on the behavioural response of prey to predators. It would not be efficient for a raptor to waste time through unsuccessful attacks. Although Jeschke et al. (2002) acknowledge this possibility, they consider attack efficiency a constant.

However, there is reason to believe that, due to prey responsiveness, attack efficiency increases as a function of prey density. The mechanism would be as follows. Falcons are forced to conceal their attacks in order to break prey defences like vigilance behaviour (Brown and Kotler 2007, Cresswell 2008). Flocking increases safety as individuals may share vigilance, and may confuse predators when attacked (Krause & Ruxton 2002, Caro 2005). It is plausible that at low densities, flocks of potential prey tend to operate as one vigilant stronghold, restricting foraging to sites where they are safe from predators. However, at higher densities, competition increases which may cause flocks to break apart. In this way, individuals that are less skilful in competitive foraging are better off in places with fewer competitors. This not only provides a raptor with more opportunities for surprise attack (i.e. it can alternate catching attempts between separate flocks – Lima *et al.* 2002), it also brings more birds in places were chances of successful attack are higher. Therefore, attack success may increase as more birds become intrinsically vulnerable as they are ‘expelled’ from the safer principal feeding grounds (Fig. 10.2 A and B).

While an increase in prey density may increase attack efficiency, an increase in falcon density decreases attack efficiency, due to mutual interference between individual raptors when approaching prey. Anti-predation responses of the prey to the presence of the predator can be called ‘prey depression’ (Yates *et al.* 2000). It is probably even stronger in falcons than it is in many other birds that visually hunt for mobile prey such as Redshank *Tringa totanus* (Goss-Custard 1980). So, if a falcon would be accompanied by a competitor, in order to achieve its minimally required intake rate it would demand higher bird densities (Fig. 10.2A; Brown & Kotler 2007), from which, through increased competition, more separate flocks could emerge. This leads to the aggregative response: the number of predators as a function of prey density (van Gils & Piersma 2004, van der Meer & Ens 1997) that is shown in Fig. 10.2 C. This explains that falcons tend to follow bird flocks (to secure sufficient prey densities) and monopolize hunting potential through aggression towards potential competitors (Chapter 4).

Predation rate at high densities may become limited by either eating (handling), or digestion, or satiation. Whether the predation rate at increasing prey densities becomes limited by digestion or (just) satiation depends (at least) on the rate and efficiency of digestion. Hilton *et al.* (1999b) note that, compared to other species, falcons and other avian raptor species have relatively few gut masses and short retention times. This would relate to the fact that they pursue active prey: as low gut masses and short retention times reduce the mass of tissue and digesta carried, it improves the linear and turning speeds needed for attack (Karasov & del Rio 2007; Chapter 9). By plucking their pickings, falcons spend relatively much time preparing bird prey

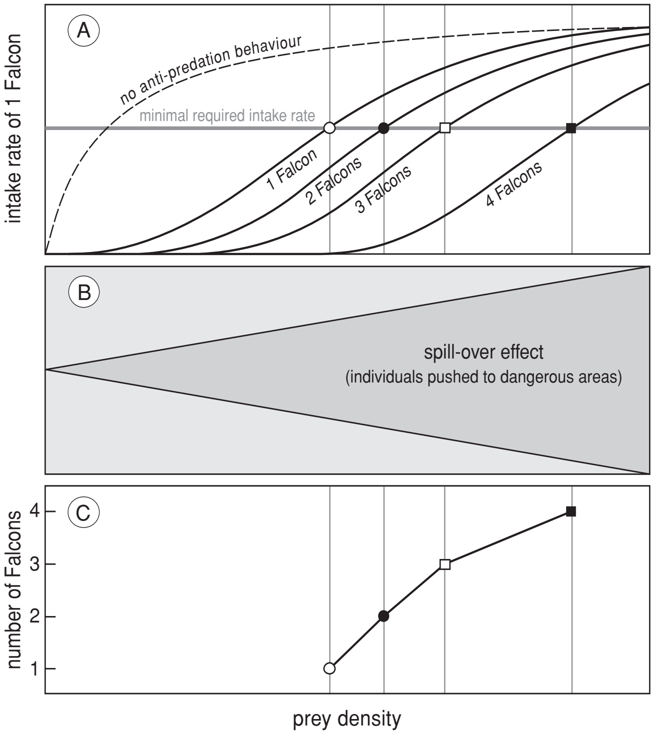


Figure 10.2 A: The functional response of a predator depends on the density of prey. As prey responsiveness decreases attack success (i.e. a predator scares away potential prey) competition by other predators increases the prey density that is required for a single predator to achieve sufficient intake rate to balance its energy budget. I propose that in the absence of anti-predation behaviour a type II response would apply (the dotted line). The open circle refers to the prey density that a falcon requires to stay in energy balance if no other falcons interfere with its foraging activities. The closed circle, open square and closed square show the minimal prey densities a falcon requires in the presence of increasing competitor numbers. B: This panel illustrates that with increasing prey density, more prey individuals are forced to forage risk-prone. C: The aggregative response of a falcon corresponding to none, one, two, three and four competitors. The saturating shape of the curve that could be fitted through the points indicates a maximum number of falcons that can subsist on ever increasing numbers of shorebird prey, assuming that at high densities shorebirds become limited in total space and therefore in the patchiness of their distribution.

for consumption. Yet, this provides them with high quality food (little wastage) to digest, which might compensate for a rapid, yet inefficient digestion (Hilton *et al.* 1999). Still it remains unclear if or to what extent a digestive constraint can limit the predation rate of a falcon whose daily food intake is aimed at maintaining energy balance.

So, interference and social intolerance are likely to strongly limit the numbers of falcons that can hunt in a given area (Newton 1998). This corresponds to the very low predator to prey ratio, which is typical for falcon-shorebird relationships, and which we also found at Banc d'Arguin (Chapter 4).

The ability of the predator to regulate prey populations below what prey resources would permit, is determined by the combined effect of functional and aggregative responses. Low falcon-shorebird ratio, prey depression, high saturation values (falcons eat relatively large prey), and the apparent absence of hoarding, at least at Banc d'Arguin (Bijlsma 1990; pers. obs.), together form a logical explanation for the low predation rates that we found at Banc d'Arguin (Chapter 4), which renders it unlikely that falcons regulate shorebird populations here. Together with the relatively high encounter probability with prey it may also explain why falcons can afford to largely restrict hunting to places where prey is most vulnerable and attacks can be best concealed (Chapters 4-6).

So, given such low predator-prey ratios, how can there be an impact of predation?

WHY MORTALITY PER SE IS A POOR PREDICTOR OF PERCEIVED PREDATION DANGER

It should have become clear from the thesis that the fact that few individuals are killed in our system does not imply that raptors would have minor impact on shorebird populations. As Lima & Dill (1990) quick-wittedly illustrate: "Consider the behaviour of people crossing a busy street. One might observe their behaviour for many days without ever witnessing a person being struck by an automobile. Could it therefore be concluded that the risk of being "preyed upon" by an automobile is unimportant in determining the behaviour of pedestrians? The answer is obviously in the negative. Of course, people carefully assess the potential for "predation" before crossing the street; if done properly, no one would ever be struck."

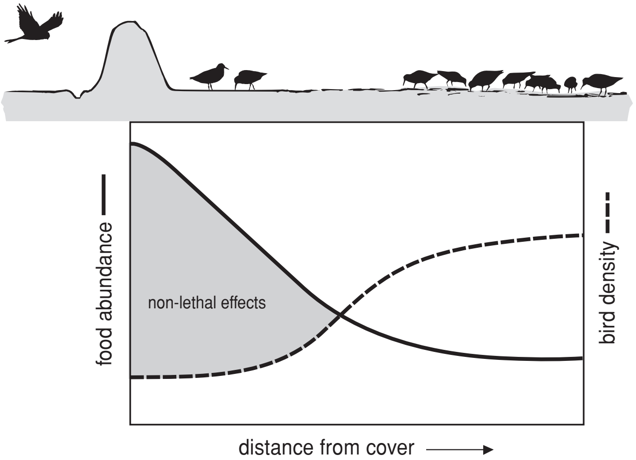


Figure 10.3 A simple example of a non-lethal effect of predation. The mere presence of raptor-concealing cover reduces profitability of foraging patches which may lead to under-exploitation of these patches (shown by the shaded region).

Yet, to add to this metaphor, the more traffic, the more time and effort it takes for pedestrians to reach their destination because they must spend more time on wariness. Wariness is just one example of an anti-predation measure, as predator-induced phenotypic changes can be developmental, morphological, physiological or behavioural (Werner & Peacor 2003). However, all these measures (which reflect the non-lethal effects of predation) have one attribute in common: they come at a cost that eventually bears on long-term survival or reproduction (Preisser *et al.* 2005, Cresswell 2008). For instance, avoiding predators in place or time goes at the expense of foraging opportunities (Fig. 10.3); time dedicated to vigilance during foraging is costly because it cannot be spent on searching for food; flocking, as illustrated in Chapter 2 and 4, had obvious benefits, including shared vigilance (freeing time for foraging), risk dilution and predator confusion (Krause & Ruxton 2002, Caro 2005), but may lead to intake depression due to interference competition (Vahl *et al.* 2005) or perhaps exploitative competition on a longer term (Goss-Custard 1980). Apart from such behavioural anti-predation measures (Chapter 2, Part II), animals may adjust body state to changing levels of predation danger (Part III). Although, for instance, a reduction in body mass increases escape chances in birds due to higher manoeuvrability, it is also costly as it reduces fat load that acts as a buffer against starvation in case of unpredictable feeding conditions.

That mortality *per se* is a poor predictor of the danger as perceived by prey, also follows from the 'predator pass-along effect' (Lima 2002), implying that individual prey that successfully evades a predator attack, 'passes the predator along' to other prey individuals, thus enhancing anti-predation responses in the prey population. In this way, foragers, even when isolated, can nevertheless interact with other (flocks of) foragers through prey-induced movements of the falcons. The extent to which predation danger is transferred within flocks obviously depends on attack success. As we have seen (Chapters 4 and 5), falcons at Banc d'Arguin appear to largely restrict their hunting to areas relatively close to the shoreline. Attack successes on these near-shore foragers prevent danger transfer to other birds, which saves energetic costs of disturbance. As for Red Knots, it also allows the majority of birds to maintain their regular foraging routines on the seagrass beds, their favourite microhabitat, which extends over vast areas predominantly far from shore, while this predictability remains largely unexploited by predators (Lima 2002).

AVOIDANCE OF PREDATORS AND EVASION OF DEPREDATION

Predators generally grant no second chance to their prey after a failed escape. Therefore, in view of the fatal fitness consequences of being depredated, predation must generally exert strong selective forces over evolutionary time on the development of mechanisms to avoid predators or evade depredation (Lima & Dill 1990). Across the animal kingdom this is reflected by a high diversity of morphological traits to avoid detection (crypsis), deter predators (aposematic coloration), or ward off predators (armour, chemical defences) (Caro 2005). Predation may also have contributed to the evolution of sociality, in- and outside the breeding season (Krause & Ruxton 2002), and in reproductive strategies (e.g. nest sites and timing of breeding, Caro 2005) and migration strategies (avoidance of predators in time and place; Lank *et al.* 2003).

Traits differ in the degree of flexibility to changes in predation danger. In many species cryptic coloration, although a fixed adaptation to a certain environment, is generally sufficient for a way of life with limited mobility or environmental change. However, if anti-predation defence is costly, and predation danger varies over time, animals should have flexible defences. Such anti-predation flexibility may be achieved by integrating morphological adaptations with behavioural decision-making (Lima & Dill 1990).

Animal decisions in the face of predation are thus based on the assessment of the associated danger in view of environmental characteristics. This implies that, in order to maximize fitness, the animal must weigh the benefits and costs of various behavioural options in terms of danger of both predation and starvation. This can translate into mechanisms to avoid predators, or to evade depredation when attacked. Brodie and Formanowicz (1991) noted that predator-avoidance and anti-predation mechanisms on attack are under somewhat different selection regimes. To illustrate this with an extreme case, selection pressure on anti-predation behaviour on attack cannot occur if predator-avoidance mechanisms are so successful that potential prey would never encounter a predator. The authors recognize that complete avoidance must be uncommon in nature, and that it is likely that both mechanisms contribute to survival in natural systems. Interestingly, the bivalve prey of shorebirds themselves are an extreme case of little or none anti-predation behaviour upon attack; yet, they have extreme predator-avoidance abilities.

In coastal shorebirds avoidance opportunities are inevitably limited as their foraging patterns are temporally and spatially determined by the tidal cycle. So, we expect both predator-avoidance and anti-predation mechanisms to contribute to their survival. Yet, for prey, selection on avoidance behaviour, through skills in foraging and competitiveness allowing the use of the safest foraging sites, even when food may be harder to find there, may be the most important (Cresswell 2008; Chapter 5). This tallies with the idea that in our study system on the Banc d'Arguin, poor foragers that were constrained in adopting the avoidance strategy, were most vulnerable to predation (Chapters 4-6).

MASS-DEPENDENT RESPONSES TO PREDATION DANGER

The way birds adjust body state to predation danger depends on opportunities they have for predator avoidance. Obviously, the fewer opportunities available for avoidance, the higher the need to be prepared for predator attack. Essentially, if not for migration, energy stores are maintained in anticipation of unpredictable feeding conditions, and thus to avoid starvation. However, as energy stores lead to higher body mass, they also entail decreased flight performance, which in case of attack by a predator could be fatal (Hedenström and Alerstam 1992, Witter and Cuthill 1993). So, individuals can respond to an increase in predation hazard by reducing body mass (but at the cost of energy stores), thus managing predation danger by reducing their foraging exposure time and ⁄or increasing their flight capacity and escape chance when attacked (the so-called mass-dependent predation risk (MDPR) response). This actually was observed in our experiments with Red Knot *Calidris canutus* (Chapter 9), while a number of other experiments, predominantly with passerines, show a similar response (Carrascal & Polo 1999, Gentle & Gosler 2001, MacLeod *et al.* 2005a, 2005b).

Yet, it is proposed that when food conditions are favourable, birds may respond to increased predation danger by avoiding foraging at times and in places of higher predation danger, at the same time *increasing* energy stores to compensate for the restricted foraging opportunities and corresponding increased starvation risk (the interrupted foraging (IF) response; Houston & McNamara, 1993, Lilliendahl 1998, Pravosudov & Grubb, 1998, McNamara *et al.* 2005, MacLeod *et al.* 2007). Some experiments were claimed to support the IF response concept (Lilliendahl 1998, Pravosudov & Grubb 1998, McNamara *et al.* 2005).

However, comparisons between MDPR and IF responses may be precarious if the circumstances of the predator-prey interactions are not taken into account. In fact, foragers *as a rule* interrupt their activities when facing a predator, while the corresponding mass-responses may occur over different time-scales. All IF responses were claimed in experiments involving small passerines that were exposed to short-term changes in predation danger and corresponding mass-responses in a diurnal context (McNamara *et al.* 2005). Indeed, also in nature, small passerines were shown to adjust their mass peak within their daily rhythm (Gosler *et al.* 1995, MacLeod *et al.* 2005a), but on a longer term the same bird may show decreasing trends in body mass (McNamara *et al.* 2005), as was shown for Great Tit *Parus major* (Gosler *et al.* 1995). Likewise, Golden Plovers *Pluvialis apricaria* decreased their strategic midwinter energy stores over a three decade period in which Peregrine Falcon *Falco peregrines* and Goshawk *Accipter gentilis* numbers greatly increased (Piersma *et al.* 2001). Meanwhile, a similar pattern has been found for Lapwing *Vanellus vanellus* (Piersma, unpubl. data). In fact, the appearance of a predator not only acts as an interruption of foraging, but also provides information about future predation danger. Therefore, responses in body state may depend on the assessments of the dangers of predation and starvation over a longer time period (Lima 1986, McNamara *et al.* 2005).

In any case, an IF response may be less likely in shorebirds that forage in intertidal areas, because (a) the tide interrupts their foraging anyhow (van Gils *et al.* 2005c), and (b) due to the openness of the mudflats they lack the refuge that small passerine have in the form of vegetation (Lind 2004, Kullberg & Lafrenz 2007). This means that intertidal foragers are constrained in adjusting their foraging in time and place to prevailing levels of predation danger. In Chapter 4 we show that shorebirds may limit exposure to predators by concentrating their foraging as much as possible on far-shore mudflats, which are rarely visited by falcons, restricting their activities in places near-shore where danger is imminently high. But, due to the limited foraging period allowed by the tide, complete avoidance of raptors by reducing foraging time is virtually impossible. Instead of seeking refuge in vegetation, shorebirds from open habitat can only find refuge among flock mates. We propose that only a MDPR response would fit in such a scenario (Chapter 9).

HOW ESCAPE TACTICS MAY DETERMINE MORPHOLOGICAL ADAPTATIONS TO PREDATION DANGER

Although reductions in body mass might reflect responses to predation danger through the MDPR response (Lima 1986, Witter & Cuthill 1993), flight performance is not only governed by wing loading (body weight divided by wing area), but also involves power output for flight, which is generated by the pectoral muscle complex (Chapters 7 and 9). The majority of studies on mass-dependent predation risk are based on body mass estimates only, without considering compensatory effects of pectoral muscle (but see Lind & Jakobsson 2001). For instance, birds were shown to adjust pectoral muscle mass to body mass changes when fuelling for migration (Dietz *et al.* 1999b, 2007). In Part III we demonstrate the ability of birds to flexibly adjust body components to changes in predation danger, and that they can either choose to increase pectoral muscle output for fast flight, or decrease body mass for manoeuvrability. We observed that Red Knots as a rule avoid foraging in places where raptor-concealing cover is close, while other species, such as Ruddy Turnstones *Arenaria interpres*, are much less reluctant to feed in such near-shore habitat (Metcalfe 1986). Their escape tactics differ accordingly, Red Knots seeking safety among flock members in socially-coordinated escape, while Ruddy Turnstones tend to freeze or escape alone or with relative few flock members into nearby safety of water or salt marsh (Chapter 9). We provided indications that species-specific changes in body composition (a decrease in body mass in Red Knot, an increase in pectoral muscle size in Ruddy Turnstone) correspond to their escape modes which are in turn related to their typical habitats (Chapter 9).

CONSTRAINTS TO ESCAPE ROUTINES

Still, birds may forage in microhabitats not suited to their escape tactics, either because they cannot cope with the rigours of foraging in certain micro-habitats and competition with dominants, or because this habitat serves their state, such as when they prepare for migration (Chapter 5). Particularly for open-habitat species, which have limited scope for predator-avoidance, this should have implications for the ways they prepare their body composition for the contingency of attack. When examining how body state relates to habitat choice, we must realise that body mass is a state with two faces, which birds are expected to optimize (Witter and Cuthill 1993, MacLeod *et al.* 2005a). Both ways, animals with low body masses may be expected to feed at riskier sites than animals with higher body masses, but, unless body state is the result of a bird eating into its fat stores, the underlying mechanism may not always be clear. It may concern an animal that seeks to improve its energy state, thereby accepting more risk in order to get a higher energy intake (Chapter 5), but it can alternatively regard an individual that chooses to be light, when feeding conditions are favourable and predictable or predation danger high, benefiting from a lower mass-dependent predation danger (MacLeod *et al.* 2008).

We know that fuelling Red Knots up to a certain level can adjust pectoral muscle to body mass increase, but at high levels they fall short in pectoral muscle adjustment with consequences for manoeuvrability (Dietz *et al.* 2007). Such heavy birds may be particularly vulnerable to predation and this is what may have happened in early June 2008, on the island of Trischen in the Wadden Sea of Schleswig-Holstein, Germany. Here, Monika Dorsch, the warden, found 22 Red Knots in full summer plumage that were caught during their spring migration and hoarded up by breeding Peregrines (Fig. 10.4).

Not so far from where these unfortunate Red Knots were found, on the island of Helgoland, Volker Dierschke had collected passerines that were caught by raptors and cats during autumn migration. Other than with the Red Knots, he found that most victims were lean birds. He concluded that lighter birds were killed disproportionately because they spent more time feeding and/or do so in more dangerous habitats. The heavier birds were safer from predators despite their hampered manoeuvrability, as they could afford to feed in safer areas away from predators (Dierschke 2003). Although Dierschke wrongly concluded that mass-dependent predation danger was therefore ecologically not important (Lank & Ydenberg 2003), this study underlines our view, as conveyed in Chapter 5, that skills in foraging, competitiveness and sociality enable birds to achieve a sufficient energy state allowing them to minimize foraging in places where they are exposed to predation (see also Cresswell 2008). However, it also shows that fuel load entails lower predation costs for birds that can escape from predators by hiding (mostly passerine species, as in Dierschke's study), than for open-habitat species, like the Red Knot, which are restricted in avoiding confrontations and therefore largely rely on escape flight in the open (Chapter 9).

Such differences in predation danger should have consequences for migration strategies. It should, for instance, necessitate Red Knots to fuel quickly in order to minimize exposure to predation hazard (Piersma 1987, 2007). Indeed, it appears that fuelling rates of Red Knots at this 'departure gate' to the breeding grounds are significantly higher than elsewhere along the flyway (Piersma *et al.* 2005). In any case, particularly in migrants that cannot use refugia, predation danger may strongly influence the decisions to either use or skip stop-over sites (Dierschke 2003, Lank *et al.* 2003, Pomeroy 2006, Leyrer *et al.* 2009).

Figure 10.4 Prey collected by Peregrines of the island of Trischen (Schleswig-Holstein, Germany). These were found on 9 June 2008 on a small observation tower and included 22 Red Knots, 3 Dunlins, 5 Woodcocks, 1 Ruddy Turnstone, 1 Sanderling, 1 feral pigeon, 1 Water Rail, and 2 Common Starlings. The Red Knots lay close together and appeared to have been killed about 2-3 weeks before they were found. (Nearly) all birds were in breeding plumage and most of the birds were largely left uneaten. The colour-ringed individual was mistnetted at the Atlantic coast of France on 6 May in the same year (see Leyrer *et al.* 2009).

Yet, as socially escaping species like Red Knot would be competing with flock mates for agility (as explained in Chapter 9), we expect birds to cope with a dilemma (as in game theory) when they fuel. Birds that fuel earlier than most others would gain the advantage to arrive earliest at the breeding grounds which would allow them to choose the best territories. However, they risk being less manoeuvrable than flock mates, and thus increase their chances of being depredated before departure!

EFFECTS OF TOP-PREDATORS ON INDIVIDUALS, POPULATIONS AND COMMUNITIES

In this thesis we propose that falcons generally exert minor mortality effects on most shorebird species, but that these lethal effects may be largest in species whose foraging specializations lead them to forage in more dangerous habitat (Chapter 4), and in age-classes that due to their inability to cope with the rigours of foraging and competitors, have limited access to the safest foraging sites (Part II). The impact of this mortality on population dynamics is further mitigated by the fact that victims are generally birds that have low reproductive value, because of their age and inferior abilities.

We provide evidence that these minor mortality effects, and the bias towards classes of birds, were caused by a combination of at least two mechanisms: (a) through anti-predation behaviour most individuals succeed in effectively avoiding predation, e.g. by minimizing encounter with predators by foraging in safe places and/or with many conspecifics; (b) due to inferior abilities in foraging and competitiveness, inexperienced birds are forced to accept higher predation danger; instead of passing the predator along (by successful escape) they appear to divert most attacks from conspecifics. It follows that safety from predators is best warranted by the development of abilities in foraging and competitiveness that enable birds to optimize energy state, through which they can afford to forage and rest at times, places and with suitable numbers of companions so as to minimize predation risk (Chapters 4-6).

We came across the paradoxical situation that raptors, like other fierce top-predators, due to their lethal capabilities, even when living amongst a wealth of prey throughout the year (a large number of shorebirds oversummer at Banc d'Arguin), are constrained in building up large local populations (Brown and Kotler 2007). This has consequences for community ecology as in such so-called 'fear-driven' systems (Box II), in which predators are not able to regulate shorebird populations, anti-predation measures reduce mortality rates and thus the amount of energy that is moving up the food chain (Trussell *et al.* 2006).

Paradoxically, predators, through the behaviour-mediated effects on their prey, may also decrease competition among foragers (Kotler and Brown 2007). When juveniles – by foraging in near-shore habitat – were able to escape from competition by dominant conspecifics, this was due to the fact that predators discouraged the latter to forage in these places (Chapter 4-5).

In Chapter 6 we show that with age Red Knot are increasingly able to forage in safe area. In view of the results conveyed in Chapter 5, it is likely that competitive foraging skills underlie this pattern, and that individuals aim to forage in patches where they can best minimize danger of predation per net rate of energy gain (Werner and Gilliam 1984). Further studies are needed to prove whether indeed such distributions based on age-related competitive abilities emerge (Parker and Sutherland 1986). Such patterns might be facilitated by environmental conditions. The small home ranges and high site fidelity and high gregariousness of Red Knots on the Banc d'Arguin (Leyrer *et al.* 2006) promote social dynamics (birds get to 'know' each other) that may easily lead to stable linear dominance hierarchies (Chase *et al.* 2002). Such hierarchies are promoted by positive feedback to initial wins and losses during hierarchy formation, i.e., when an animal dominating in one contest goes on to dominate in others and when an animal becoming subordinate in one contest continues to be subordinate in others. This mechanism may lead to a distribution where birds use the knowledge of dominance ranks to distribute themselves in such a way as to mitigate competition in favour of feeding efficiency (Leyrer *et al.* in prep.).

Yet, the degree of structuring in flocks may depend on the season. As many other long-distance migrants, Red Knots have staggered movements by males, females and juveniles (Myers 1983), and, together with a high mobility during migration, this makes highly structured associations less likely, at least at staging sites during migration. However, a higher potential for self-organisation is likely to arise when birds settle in their winter quarters (Leyrer *et al.* in prep). Furthermore, we suspect that in areas in which birds have larger home ranges, for instance due to unpredictable feeding conditions, bird aggregations may be more fluid. This may occur in temperate areas were sudden drops in temperature negatively affect feeding conditions (Leyrer *et al.* 2006), and in areas that are disturbed, e.g. by anthropogenic influences (van Gils *et al.* 2006b). We suspect that in such areas, birds have to deal with more aggressive confrontations at the expense of feeding efficiency.

Through avoidance behaviour of individuals, the effects of predation may extend to the field of community ecology, because patterns of competition release by predators also occur between species. Differential individual decisions in balancing costs and benefits of habitat use, may lead to differences in habitat use (Kotler and Brown 2007). This may eventually force species that were strong competitors in the past into different realized niches, allowing for their coexistence (Cresswell 2008).

Only when they show their spectacular hunting skills, predators are awesome. Most of the time they are boring, elusive creatures lurking behind the scenes for a chance to get a meal. It is essentially through the fear they create, that predators have such tremendous influence on the structure and dynamics of shorebird populations and communities.

EPILOGUE

… it took remarkably short for the panic to subside and within a few minutes the crowds reorganized and proceeded with the ceremony, seemingly untouched by the disturbances. Just as the zebra's would resume their peaceful grazing after finding out that it was just a breeze in a bush, and the shorebirds quickly recovered from their jumpy response, unconsciously aware that predation is something they just have to learn to live up with.

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Summary
Samenvatting

SUMMARY

Some decades ago, through use of pesticides, falcons and other shorebird predators had become quite rare in many intertidal areas throughout Europe. Since the end of the 1970s, through the banning of pesticides, a dramatic recovery set in. From then on, shorebirds in the Wadden Sea have progressively been confronted with falcons, at first only during the winter season, but increasingly also in spring and summer as falcons has established themselves as breeding birds. Nowadays, particularly in the non-breeding season, virtually no shorebird roost in the Wadden Sea escapes the attentions of one or two falcons. These attentions are not limited to the temperate regions, as the millions of shorebirds that migrate to their African winter quarters, such as Banc d'Arguin, Mauritania, are faced there with these specialised bird hunters as well.

In this thesis the impact of these top-predators on shorebird populations and individuals are investigated. Controlled experiments at the Royal Netherlands Institute for Sea Research (NIOZ) were combined with field observations. Most observations were conducted at Banc d'Arguin. Apart from being such an important wintering site for shorebirds along the East-Atlantic Flyway, the high site-faithfulness and relative small home ranges of species at Banc d'Arguin, made systematic research on raptor-shorebird interactions much easier than in the Wadden Sea (Box I).

The investigations on the impact of predation on shorebirds started with examination of relative vulnerabilities of species and age-classes. Combining prey remains with hunting intensity revealed that direct mortality due to predation was generally low (in most species not more than 1-2% of the local wintering population). As for Red Knot *Calidris canutus*, not more than 6% of the overall yearly mortality of juveniles, and less than 1% in adults, could be explained by predation. However, low predation mortality is no proof of low impact. Instead, it can be an indication that by effective anti-predation behaviour most individuals avoid being depredated (Chapters 5 and 6).

Large differences in predation mortality between classes of birds reflect differences in vulnerability: for some reason certain individuals seem constrained in their abilities to fend off depredation. For instance, species that habitually forage in nearshore area seemed more vulnerable than species that as a rule avoid nearshore habitat (Chapter 4). This corresponds to the hunting techniques adopted by the local falcons: these utilize the low dunes bordering the mudflats to launch surprise attacks on inattentive individuals. In three species (Bartailed Godwit *Limosa lapponica*, Red Knot and Dunlin *Calidris alpina*) it was shown that juveniles were much more vulnerable than adults (Chapter 4). In Red Knot we connected this to the question where, when and with whom they foraged. This revealed that although the vast majority of Red Knots tended to avoid shorelines as much as possible, small groups were observed foraging in nearshore habitat throughout the tidal cycle. These birds were predominantly young.

Why would any bird take such risks? This is the central question in Chapter 5. We provide indications that, through inferiour abilities in foraging skills and competitiveness, some young Red Knots cannot afford to feed with the principal flocks in areas where they would be relatively safe from predation. Some individuals may even be better off foraging in places where food is less abundant, but easier to find and handle, and with fewer competitors, despite higher predation pressure.

This triggers questions as to the quality of such individuals: are they predominantly low quality birds that will die anyway, or are most birds gradually making their way up to safer foraging conditions? This question was investigated by monitoring habitat use from year to year of individually marked birds in relative age-classes up to 11 years old (Chapter 6). Results from this analyses support the scenario that, although more birds may get killed in dangerous habitat, with age many birds increasingly avoid dangerous foraging locations, which suggests they go through a learning process. The findings in Chapters 5 and 6 support the idea that natural selection acts upon abilities in foraging and competitiveness, as these enable birds to avoid predation danger in time and space as much as possible.

Shorebirds were shown to match the intensity of their anti-predation response (in escape flight, vigilance and feeding) to the degree of threat posed by predators (Chapter 8). Nevertheless, even the shorebirds that manage best in avoiding direct encounters with predators are inevitably confronted with attacks once in a while. And, as one failure to escape attack is likely to be fatal, birds have to be prepared for escape at all times. Therefore, particularly when dealing with highly mobile predators, such as falcons, weight-watching in birds is probably even more vital for survival than it is in humans. Although fat stores protect birds against starvation, they may decrease their escape performance. Experiments with fuelling Red Knots demonstrated that – up to a certain body mass – a decrease in flight capacity due to extra fuel load is compensated by putting on extra pectoral muscle ('flight muscle'). Therefore, it is expected that birds likewise utilize such 'phenotypic flexibility' in case of predation danger, either by increasing pectoral muscle or by decreasing overall body mass; both resulting in a relative increase in pectoral muscle, thus an increase in flight capacity. We tested this idea in our bird facilities at NIOZ, by exposing small flocks of Ruddy Turnstones *Arenaria interpres* to a raptor model (Sparrowhawk *Accipiter nisus*) gliding overhead at unpredictable times, applying a Black-headed Gull *Larus ridibundus* as a control (Chapter 7). Indeed the Ruddy Turnstones increased and decreased their pectoral muscle upon exposure to raptor and gull respectively. We repeated this experiment with Red Knots, hypothesizing that Red Knots, just like Ruddy Turnstones, would respond to predation danger by an increase in flight capacity, though not by an increase in pectoral muscle, but by a decrease in overall body mass (Chapter 9). This idea was triggered by differences in habitat use and social behaviour between Red Knots and Ruddy Turnstones. Ruddy Turnstones generally forage in the proximity of shorelines, thus close to raptor-concealing cover. As predator detection often occurs when the raptor is already very close, a rapid acceleration is essential for timely escape to vegetation, to a water surface, or to build up enough speed for maneuvers. In order to generate such acceleration, power for flight should be first priority, and this may explain why Ruddy Turnstones increased pectoral muscle size upon raptor disturbance. Red Knots, on the other hand, as a rule forage far from raptor-concealing structures, such as dunes and dykes. This generally enable detection of a raptor at greater distance, which gives Red Knots more time to gain height and speed and recruit flock members for coordinated fast-swerving escape. Based on aerodynamic properties of flight, we calculated that with sufficient speed the executions of fast and sharp turns depend on body mass alone. Therefore, in response to increasing predation danger Red Knots should lower body mass, and this is what they did in our experiment (Chapter 9).

These experiments demonstrate some morphological adjustments birds are capable of, and how escape tactics may depend on species-specific traits such as habitat use and corresponding social behaviour. Such responses may be difficult to detect under natural conditions, as they may be integrated in compensatory behaviours. For instance, although birds with higher fat loads are probably less proficient in escape, they may compensate for this by restricting foraging at times and in places with less predation danger – if they can afford doing so.

In conclusion, safety from predators seems to be best warranted by the development of abilities in foraging and competitiveness that enable birds to optimize energy state, through which they can afford to forage and rest at times, places and with enough flock mates so as to minimize predation risk.

SAMENVATTING

In de jaren zeventig en tachtig waren valken en andere wadvogelpredatoren door het gebruik van pesticiden in veel waddengebieden zeer zeldzame verschijningen geworden. Inmiddels zijn, om het dicht bij huis te houden, Slechtvalken *Falco peregrinus*, als doortrekkers, wintergasten en hier en daar zelfs als broedvogels, vaste gasten op bijna elke wadplaat in de Waddenzee. Maar ook op de Banc d'Arguin, waar miljoenen steltlopers uit Hoog-Arctische gebieden overwinteren, hebben steltlopers met dergelijke gespecialiseerde vogeljagers te maken.

In dit proefschrift wordt onderzocht wat de aanwezigheid van valken betekent voor steltlopers. Experimenten op het NIOZ, onder gecontroleerde omstandigheden, worden gecombineerd met veldobservaties. Het veldonderzoek spitst zich toe op de Banc d'Arguin, dat niet alleen van groot belang is voor steltlopers, maar waar deze, in tegenstelling tot de Waddenzee, ook zeer plaatstrouw zijn, wat studies van prooi-predator relaties een stuk gemakkelijker maakt (Box 1).

Bij de vraag naar de betekenis van predatie door valken op steltlopers ligt het voor de hand eerst onderzoek te doen naar de vraag welke proportie van een populatie, per soort, door valken wordt geconsumeerd. We onderzochten dit door gevonden prooiresten te combineren met waarnemingen van jachtintensiteit (Hoofdstuk 4). Het bleek dat directe sterfte door predatie in het algemeen zeer gering was (voor de meeste soorten niet meer dan 1–2% van de winterpopulatie). Voor Kanoeten konden we niet meer dan 6.2% van de algehele jaarlijkse mortaliteit van jonge vogels en 0.8% van oudere vogels verklaren door predatie in hun wintergebied. Echter, lage sterfte door predatie laat onverlet dat de invloed van predatie op individuen groot kan zijn. In feite kan het een aanwijzing zijn dat de meeste individuen zich door effectief anti-predatiegedrag aan predatie weten te onttrekken (Hoofdstukken 5 en 6).

Grote verschillen in predatiesterfte tussen klassen van vogels duidt op verschillen in kwetsbaarheid: kennelijk zijn bepaalde individuen door een of andere oorzaak beperkt in hun mogelijkheden om predatiegevaar af te wenden. Analyse van prooiresten in vergelijk met tellingen van vogels in het studiegebied suggereerde dat soorten die de gewoonte hebben dichter aan de kant te foerageren vaker slachtoffer worden dan soorten die de kanten juist zoveel mogelijk mijden. Dat verschil komt overeen met de jachttactieken van de valken. In ons onderzoeksgebied gebruikten de valken de kale heuvels als uitvalsbasis voor aanvallen. Vandaaruit werden de duintjes vlak langs het wad benut om argeloze vogels te overrompelen. Van drie soorten waarvan aan de hand van de vleugels (die doorgaans niet door de valken worden gegeten) kon worden afgelezen of ze eerstejaars vogels waren of ouder, konden we vaststellen dat de jonge vogels aanzienlijk vaker gegrepen waren dan de oudere (Hoodstuk 4). Voor Kanoeten konden we dat koppelen aan de vragen waar, wanneer en met wie ze voedsel zoeken (Hoofdstuk 5 en 6). Wat bleek namelijk: hoewel de meeste Kanoeten de kanten zoveel mogelijk mijden met oog op predatiegevaar, lopen er zowel bij hoog als bij laag water toch kleine groepjes vogels rond. Dat zijn voornamelijk jonge vogels.

In Hoofdstuk 5 stellen we ons de vraag waarom vogels, zoals deze jonge Kanoeten, hoe dan ook dit soort risico's zouden nemen. Ons onderzoek biedt aanwijzingen dat de jonge Kanoeten zich de 'luxe' van voedselzoeken in grote groepen op veilige plaatsen (nog) niet kunnen permitteren omdat ze minder bedreven zijn in het zoeken en verwerken van voedsel en de nodige sociale vaardigheden missen om de concurrentie met oudere soortgenoten aan te gaan. Dat kan er zelfs toe leiden dat individuen beter af zijn als ze foerageren op plaatsen waar minder voedsel ligt, maar waar het gemakkelijker te vinden en te hanteren is en waar ze minder door concurrenten worden gestoord, zelfs als het predatiegevaar daar hoger is.

Hebben we hier te maken met onaangepaste individuen die hoe dan ook spoedig aan hun einde zouden zijn gekomen, of betreft het vogels die zich vanuit een kritische periode van onervarenheid opwerken in de groep met gunstige consequenties voor veiligheid? Die vraag hebben we onderzocht aan de hand van individueel gebiedsgebruik. Door vogels te vangen en van individuele kleurringcombinaties te voorzien, konden we patronen van individueel gebiedsgebruik van jaar op jaar analyseren (Hoofdstuk 6). De resultaten ondersteunen de laatste optie: Kanoeten bleken gedurende hun leven de gevaarlijke kanten steeds meer te gaan mijden. De bevindingen in Hoofdstukken 5 en 6 maken aannemelijk dat natuurlijke selectie sterk inwerkt op vaardigheden in foerageren en competitieve kracht. Dat maakt het immers mogelijk dat vogels predatiegevaar in tijd en ruimte zoveel vermijden. Dat neemt echter niet weg dat zelfs de steltlopers die er het beste in slagen om aan confrontaties met valken te ontkomen, niet kunnen voorkomen dat ze af en toe aan aanvallen worden blootgesteld. En aangezien één mislukte ontsnapping fataal is, moeten ze te allen tijde op deze kans zijn voorbereid.

Dat is de reden waarom vogels, net als mensen, altijd een beetje op hun gewicht moeten letten. Weliswaar kan het aanleggen van vetreserves vogels tegen verhongering beschermen, het maakt ze ook minder wendbaar bij aanvallen. Uit experimenten met opvettende Kanoeten is duidelijk geworden dat – tot een zeker lichaamsgewicht – een verlies in vliegcapaciteit door gewichtstoename wordt gecompenseerd door het vergroten van de borstspieren, de spieren die voor vliegen worden gebruikt. Het valt daarom te verwachten dat vogels deze 'fenotypische flexibiliteit' ook zullen inzetten in geval van predatiegevaar, hetzij door bij groter gevaar de borstspieren wat te versterken, hetzij het lichaamsgewicht wat te laten zakken. Beide resulteren in een relatieve toename van de borstspieren en dus in een vergroting van de vliegcapaciteit. We hebben dit in een experimentele ruimte op het Koninklijk Nederlands Instituut voor Zeeonderzoek (NIOZ) getest met Steenlopers *Arenaria interpres* door groepjes vogels op onvoorspelbare tijden met een overglijdend roofvogelmodel, Sperwer *Accipiter nisus* (en een Kokmeeuw *Larus ridibundus* als 'controle') te confronteren (Hoofdstuk 7). Steenlopers – zowel als Kanoeten in een vergelijkbaar experiment – reageerden duidelijk verschillend op verschillende gevaarsintensiteiten (een meeuw- ten opzichte van een roofvogelmodel (Hoofdstuk 7), een zittend ten opzichte van een vliegend roofvogelmodel (Hoofdstuk 8)).

Steenlopers bleken hun borstspieren te vergroten en te verkleinen naargelang het gevaar groter (bij blootstelling aan het roofvogelmodel) of kleiner (bij presenteren van het meeuwmodel) werd. We herhaalden dit experiment met Kanoeten. We stelden de hypothese op dat Kanoeten, net als Steenlopers, zouden reageren op predatiegevaar door vergroting van hun vliegcapaciteit, zij het niet door versterking van de borstspier maar door verlaging van hun lichaamsgewicht (Hoofdstuk 9). We werden tot deze gedachte geïnspieerd door verschillen in habitatgebruik tussen Kanoeten en Steenlopers. Steenlopers zoeken hun voedsel doorgaans vrij dicht langs de kanten, zoals in de aanspoelzone. Daar hebben ze vaak een beperkt uitzicht op de horizon waardoor ze het risico lopen verrast te worden door een roofvogel, bijvoorbeeld een valk of een kiekendief. Omdat de roofvogel op het moment dat ze hem ontdekken meestal al heel dichtbij is, moeten Steenlopers zo snel mogelijk de veiligheid opzoeken van een wateroppervlak of vegetatie. De eerste meters zijn van levensbelang en de vogel moet zo snel mogelijk op snelheid komen om hetzij in de vegetatie te duiken, het wateroppervlak te bereiken, of te kunnen zwenken. Om die versnelling te kunnen genereren is vliegkracht een eerste vereiste en dat zou kunnen verklaren waarom de Steenlopers in het experiment hun borstspier vergrootten bij groter gevaar. Kanoeten daarentegen zoeken hun voedsel in de regel zo ver mogelijk verwijderd van structuren, zoals duintjes en dijklichamen, die het zicht op een aanstormende roofvogel zouden kunnen belemmeren. Dat betekent dat Kanoeten een roofvogel meestal al in een relatief vroeg stadium ontdekken. Dat geeft hen meer tijd om de lucht in te gaan en snelheid op te bouwen ter voorbereiding van snelle gecoördineerde zwenkingen tezamen met soortgenoten om aan de aanvaller te ontkomen. Aan de hand van berekeningen aan aerodynamische eigenschappen van het vliegen konden we vaststellen dat als eenmaal snelheid is opgebouwd succesvol bochtenwerk uitsluitend nog afhangt van lichaamsgewicht. Kanoeten moeten dus in reactie op predatiegevaar hun lichaamsgewicht laten zakken en dat is wat ze deden in ons experiment (Hoofdstuk 9).

Deze experimenten vertellen ons tot welke aanpassingen vogels in staat zijn en welke ontsnappingstaktiek een soort afhankelijk van habitatgebruik en sociale context zou kunnen kiezen. Omdat deze reacties op predatiegevaar onder gecontroleerde omstandigheden werden gemeten, laten ze niet het volledig spectrum van anti-predatieaanpassingen zien. In de natuur kunnen morfologische reacties op predatiegevaar geïntegreerd worden in compenserende gedragingen. Bijvoorbeeld, hoewel vogels met extra energievoorraden minder kans maken om bij een aanval aan een predator te ontsnappen, kunnen ze in plaats van gewichtsverlaging of spiervergroting, ter compensatie van het aan extra gewicht gekoppelde risico, hun foerageren beperken tot plaatsen en tijden met minder predatiegevaar – mits ze zich dat, gelet op hun vaardigheden, kunnen veroorloven.

Al met al lijkt de beste bescherming tegen predatie de ontwikkeling van vaardigheden in foerageren en het omgaan met concurrentie waardoor vogels een goede energetische conditie kunnen verkrijgen die hen vervolgens in staat stelt de blootstelling aan predatiegevaar zo klein mogelijk te houden.

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