Struggle for safety

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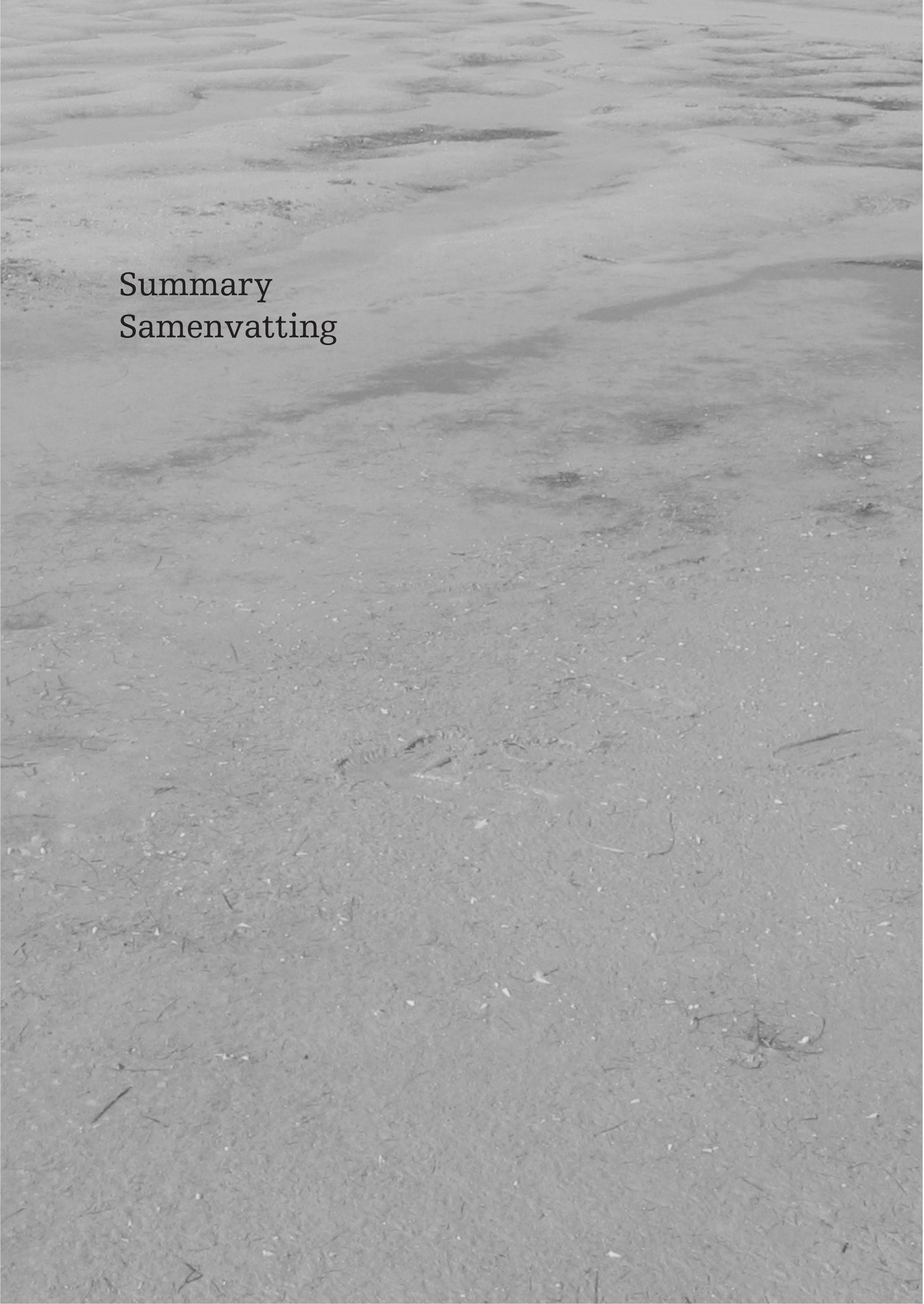
Summary
Samenvatting



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.