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Ruffs in rough times

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1

General introduction

Our ecological world is based on an amazingly intricate web of interactions among living organisms. Only too often we ignore the functional importance of all these interactions. As humans we developed our activities worldwide, putting upfront economic productivity while neglecting sustainability (Steffen et al. 2011). The environmental and societal consequences that we are facing today are major, and press us to set our priorities differently (Steffen et al. 2011). Now that a greater ecological awareness is reaching governments and international authorities (Folke et al. 2011; United Nations, 2015), it is up to everyone to lead the way towards transitions for a sustainable future. As a biologist, I hope that this thesis will contribute to a better understanding of how populations of a free-living species, and more particularly an inland migratory shorebird species, respond to the changes we, humans, induce, and will help to suggest the actions we can take to preserve them and the important habitats we share.

Endangered shorebirds migration routes connecting wetlands worldwide

Migratory shorebirds and their impressive journeys embody some of the literally far-reaching connections which exist between habitats and organisms across the Earth (Bauer and Hoye, 2014). These small to medium sized wading birds are well adapted to make long flight and often travel from tropical wintering quarters, to temperate stopovers where they rest and fuel, before heading to breeding grounds in the Arctic. These long moves allow shorebirds to track peaks of resources, good habitats and safe conditions in order to survive and breed across highly seasonal environments (Alerstam and Lindström, 1990; van de Kam et al. 2004). At each stage of the journey, they may assemble in high numbers so that as prey or as consumers they translocate nutrients and spread propagules, parasites and pathogens (Duarte et al. 2016; Bauer & Hoye, 2016; McKay and Hoye, 2016). In these ways, shorebirds enter and connect the dynamics of the ecosystems that they use: the shorelines of oceans, seas, lakes, rivers and any places where water meets the land.

In an era of rapid human-induced global changes, the integrity of these connections between wetlands is threatened, and serious concerns are growing on the future of shorebird migration. It has been estimated that 64–71% of our natural wetlands were lost since 1900 (Davidson, 2014). Today, shorebirds routinely migrate over wetlands that were converted or modified to enhance their economic potential such as providing hydraulic power, water or supporting our agriculture. Some of these man-made wetlands represent alternative habitats, but often only partially fulfil the ecological requirements of particular species compared with natural habitats (Ma et al., 2010). More indirectly, global warming also challenges shorebirds, perhaps especially on their breeding grounds. The remote and relatively untouched, arctic wetlands are strongly subjected to climate change which influences snow conditions and the regularity of predator-rodent cycles (Kausrud et al. 2008), both of which indirectly affect the reproductive output of shorebirds (Blomqvist et al. 2002; McKinnon et al. 2014). Disrupted food webs can also challenge the growth of young and smaller body size become a disadvantage later on, for instance to forage and survive during the tropical winter (e.g. van Gils et al. 2016).

Populations are responding to these changing conditions. Among others, impressive range shifts (e.g. Brommer et al. 2012), modified migratory patterns (e.g. Márquez-Ferrando et al. 2012) or phenological adjustments (e.g. Pierce-Higgins et al. 2005) are well-known responses. However, there may not be always room to adjust, when rapid alteration of critical habitats drive high individual fitness costs and lead to sudden and steep population declines. This is currently happening over the intertidal flats of the Yellow Sea which are being reclaimed at great speed for industrial development (Yang et al. 2011; Murray et al. 2012) as shorebirds of the East-Asian-Australasian flyway are losing their most important staging areas. With no alternative stopover to refuel sufficiently during migration, shorebird species using this route began to show steep population declines (Piersma et al. 2016; Studds et al. 2017). Today, shorebirds are a particularly endangered group among migratory birds showing some of the largest and most widespread populations declines worldwide (International Wader Study Group, 2003; Stroud et al. 2006).

Monitoring shorebird population changes over flyways

If we are to evaluate the future resilience of declining shorebirds populations and to provide measures adaptive management, we need to be able to understand ecological mechanisms and demographic processes underlying the changes in the numbers we observe. Counts that are carried consistently over years at given site(s) of a flyway are very often the first quantitative measure enabling to detect population changes, but they provide no information on the underlying causes. Most simplistically, any population change that we observe may be the result of a change in survival, breeding output and/or individual movements (i.e. immigration or emigration). Concerning migratory birds, the variation in these core demographic parameters may be related to conditions encountered during breeding, wintering and/or upon migrations, which themselves have either immediate or delayed effect on the behaviour and fitness of individuals (Newton, 2004). The study of population changes thus impose a major pre-requisite: being able to follow the movements and fates of a representative amount of individuals at large-scale and on long-term basis.

Although most likely they represent the future, satellite tags are still expensive and, depending on the species, possibly too invasive to enable large scale application for inferences at the population level. The most powerful approach until now remains long-term capture-mark-recapture (CMR) monitoring, allowing the demographic characterisation of free-living populations whilst accounting for the imperfect detectability of marked birds within the CMR statistical framework (see Lebreton et al. 1992). CMR monitoring programs are based on consistent efforts to capture, mark and subsequently to resight (or recapture) individuals from one or several site(s) to which birds ideally display a high degree of fidelity. This way, the observation (or recapture) of a marked individual, at a given time, confirms its survival since its capture or previous sighting. It also tells about its use of a particular site or habitat or its behavioural state. When an individual is not observed at this same given time, it may have died, emigrated permanently, or was simply missed.

On the basis of the capture histories of all marked individuals it is thus possible to compute a resighting probability (or recapture probability) given that an individual is alive and thereby reducing the risk of flawed inference on the parameter(s) of interests (Lebreton et al. 1992; Gimenez et al. 2008). According the monitoring design (i.e. when and where capture and observations occur), CMR modelling can be designed to estimate probabilities to survive, to breed (Sanz-Aguilar et al. 2011), to recruit (Pradel et al. 1996), to move between sites (Hestbeck, 1991), but also to estimate population size (Kentie et al. 2016), stopover duration (Guérin et al. 2017), breeding dynamics (Choquet et al. 2014) and many other aspects; incorporating information such as individual characteristics, behavioural states, as well as uncertainty on these states (Pradel, 2005), environmental covariates (Grosbois et al. 2008) or population size (Schaub and Abadi, 2011). The CMR statistical framework has become a robust and integrative tool to study the drivers of population changes in free-living populations.

Motivation and aim of the thesis

This PhD is inspired by the initiative of the Global Flyway Network (GFN) to build up a comparative network of research studying migratory shorebirds populations facing environmental changes (Piersma, 2007). The initiative coordinates long-term colour-ring monitoring programs on representative species along each of the world's flyways (Fig. 1.1) to investigate habitat use, individual life histories and population trajectories through time. Altogether it shapes a framework that enables inferences on worldwide scale, benefiting from insightful comparisons according to the many similarities and contrasts of shorebird annual cycles (Piersma and Davidson, 1992; Piersma 2007; Buehler and Piersma, 2008). Most emblematically, the coordinated studies on the Red Knots subspecies (*Calidris canutus*) have widely enhanced knowledge on Red Knots annual cycles (Piersma and Davidson, 1992; Piersma, 2007; Buehler and Piersma, 2008) and contributed in understanding the impact of human induced changes (e.g. Piersma et al. 2016; van Gils et al. 2016). It has been operating as a warning system that detects population decline early on, and provided feedbacks to implemented conservation measures (Piersma and Lindström, 2004). This work has been decisive in protecting coastal shorebirds and their intertidal flats at international levels (Piersma et al. 2001; Yang et al. 2011; Conklin et al. 2014).

The GFN initiative, which has so far mainly concerned coastal shorebirds is opening up to inland species, integrating the long-term studies on the continental Black-tailed Godwits (*Limosa limosa limosa*) and Ruffs (*Philomachus pugnax*) over the East-Atlantic flyway. Both species are monitored from The Netherlands where they respectively breed and stage during migration using the dairy grasslands of the northern province of Friesland. Both populations show a long lasting decline locally (Zöckler et al. 2002a; Verkuil et al. 2012a; Kentie et al. 2016). According to the available evidence, the decline of breeding Black-tailed Godwits result from insufficient recruitment due to the loss of herb-rich wet grasslands following agricultural intensification (Kentie et al. 2013, 2015). The Black-tailed Godwit is an iconic species in The Netherlands and their decline has raised much concerns translating rapidly into conservation measures to protect breeding meadow birds species in general (www.kingofthemeadows.eu). Much less attention has been dedicated to the large passage population of shorebird species and the near-disappearance of the Ruffs from The Netherlands. However, the first steps of research on Ruffs initiated in 2004, suggested that intensive management of grasslands in Friesland led to a marked decrease in the refuelling rates of staging Ruffs during spring migration (Verkuil et al. 2012a). Losing their major staging area on the East-Atlantic flyway, the western population Ruffs would have redistributed eastwards, hereafter migrating through central and Eastern Europe (Rakhimberdiev et al. 2010; Verkuil et al. 2012a).

This thesis will focus on the Ruffs and aims to deepen our understanding of their decline in The Netherlands and along the East-Atlantic flyway, now that we have had more time and hindsight. Our objective was to continue the long-term capture-resightings monitoring of Ruffs in Friesland to achieve a sufficient series of years to address the demography of the recent population changes using a proper CMR statistical network. We also tried to accumulate more ecological evi-

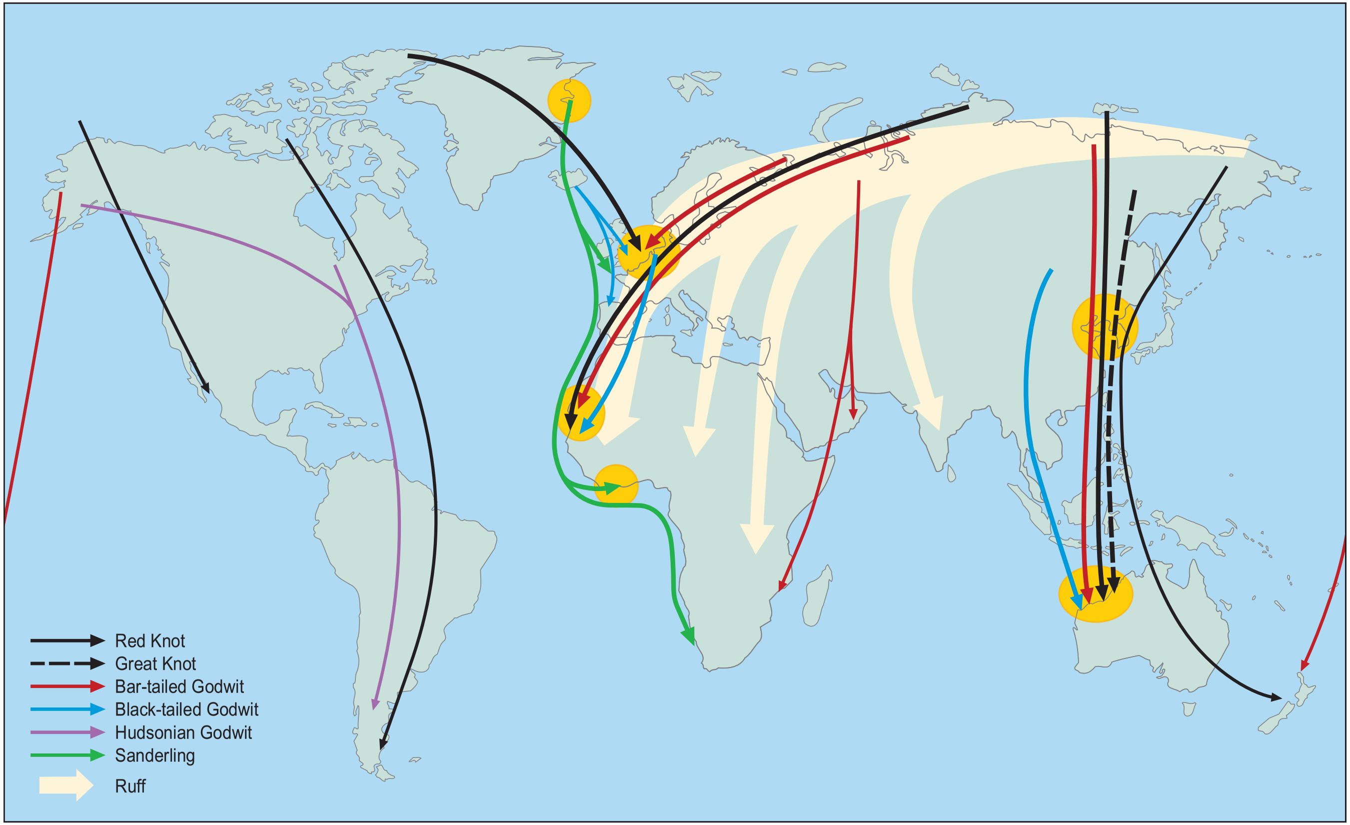

Figure 1.1: Overview of all GFN demography programs (including Ruff) with centres of research activity indicated with the yellow dots.

dence on how staging Ruffs cope and further perform in the local context including human induced changes elsewhere on the East-Atlantic flyway. Ultimately, we hope that this work will contribute to sustainable usage of freshwater wetlands and agricultural grasslands to enable shorebirds protection along this particular flyway, and we aim to contribute to the general knowledge on migratory inland wader species.

Study system : Ruffs staging in the Netherlands

Peculiar Ruffs

Ruffs are first known for their mating system: colourful males display on a lek showing their extravagant plumage to pursue females and copulate with them. Unique among birds, Ruffs present three genetically determined male morphs differing in morphology, plumage, behaviour and fertility: the aggressive colorful independent and 'semi-cooperative' white satellite males, twice as big as females and developing an elaborated nuptial plumage; and the female-mimicking "faeders" of intermediate size which, just as females, keep an inconspicuous plumage (van Rhijn 1973, 1991; Lank et al. 1995; Hogan-Warburg 1966; Widemo 1998; Jukema & Piersma 2006; van Rhijn et al. 2014 ; Küpper et al. 2016). Females are much smaller than males, and even carry a distinct name: reeves. They assume all parental care. Males migrate about three weeks ahead of the females and winter more northerly (van Rhijn, 1991). Thereby males and females live mostly apart of each other, and when present in the same environment they are even likely to exploit slightly different niches (pers. obs.; van Rhijn, 1991; Jukema et al. 2001a).

Beyond their peculiar mating system, Ruffs are a common inland shorebird species. The total population, at least 10–20 years ago, counted more than 2 million individuals over a wide distributional range (Piersma et al. 1996; Zwarts et al. 2009). The bulk of the population winters in floodplains, river sides and lakes of sub-Saharan Africa, but Ruffs can also be found in southern Asia and Indonesia (Cramp and Simmons, 1983). Smaller wintering areas exist at temperate latitudes in wetlands and wet agricultural areas of the Mediterranean basin (Qninba et al. 2006; Hortas and Masero 2012) and northwestern Europe (Prater 1973; Castelijns 1994; Gill et al. 1995; Devos et al. 2012; Hornman et al. 2013). In summer, Ruffs breed all over northern Eurasia in the tundra at Arctic latitudes, in open lowland with freshwater marshes and wet grasslands over its sub-Arctic and temperate range (Zöckler, 2002b).

Ruff migration occurs on a broad front through Europe and Asia (Zwarts et al. 2009). Over their temperate staging areas, Ruffs prefer open landscape with any kind of shallow freshwater areas, but are also strongly associated to short-sward grasslands, and agricultural crops. Major migratory flyways were identified with recoveries of ringed birds (Zwarts et al. 2009, see Fig. 1.2), but a lack of genetic structure in the global population attests to important gene flow (Verkuil et al. 2012b). Nevertheless, some phenotypic differences in wings length between West and East populations are suggestive perhaps of an evolving population structure (Verkuil et al. 2012b).

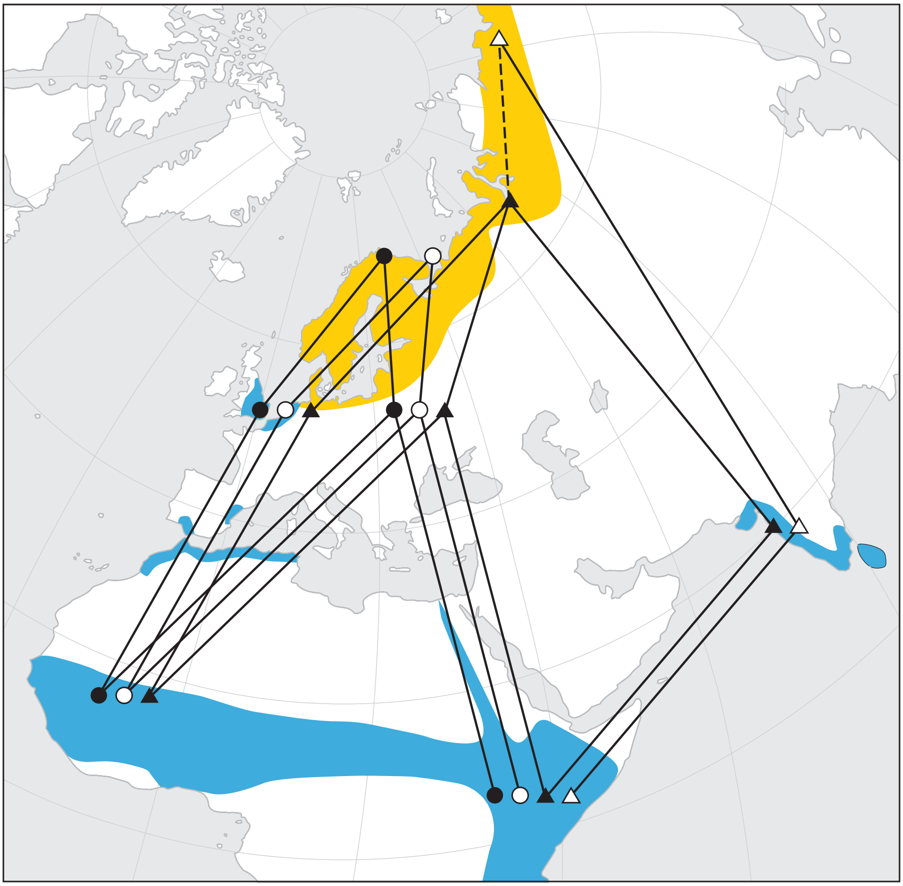

Figure 1.2: Breeding and wintering areas of the Ruff *Philomachus pugnax* and the major migration routes through Western and Eastern Europe, here indicated with lines. Wintering quarters are indicated in blue, breeding grounds in yellow. (Modified after Zwarts et al. 2009 and Rakhimberdiev et al. 2011).

On the global scale, the Ruff population is currently considered as Least Concern by the IUCN Red List. Despite the rapid decline of the European breeding population and an apparent breeding range retraction towards the Arctic (Väïsaïnen et al. 2005; Øien and Aarvak 2010; Virkkala and Rajasärkkä 2011; Lindström and Green 2013), the global population does not approach yet the thresholds of a "Vulnerable" status.

East-Atlantic Ruffs

Our main focus is here the East-Atlantic population of Ruffs. These western Ruffs used to breed in high numbers in northern temperate Europe until the 1970s, but then dramatically declined following the intensification of agriculture. Intensive drainage, increased fertilization and mechanization for a production driven agriculture had a disastrous impact on nesting success and breeding output of meadows birds (Kentie et al. 2013; Kleijn et al. 2010; Vickery et al., 2001). Particularly dependent on wet conditions (Beintema, 1986), Ruffs rapidly vanished as a breeding bird. By 1990, 90% of the total breeding population in England, France, Belgium, The Netherlands, Germany, Denmark, southern Sweden, Poland, Estonia, Latvia and Lithuania had disappeared (Thorup, 2006), and from there the decline spread into the sub-arctic Scandinavia perhaps also under the influence of climate change (Väïsaïnen et al. 2005; Øien and Aarvak 2010 ; Lindström and Green 2013). In contrast to the situation in the west, positive abundance index over western Siberia suggested a simultaneous and global redistribution of the breeding population beyond the Yamal Peninsula (Rakhimberdiev et al. 2011).

The Netherlands continued to host tens of thousands of Ruffs during spring migration until the late 1990s, after which the passage population showed a steady decline (Verkuil et al. 2012a). In the late 1990s, peak numbers of staging Ruffs exceeded 20,000 individuals. In 2010, peak numbers counted no more than 5000 birds (Verkuil et al. 2012a). This considerable drop went along with a diminution of the daily body mass increments of staging Ruffs (i.e. population wide) between 2001 and 2008, most likely explained by the deterioration of grassland habitats quality of the staging site (Verkuil et al. 2012a). In parallel to the situation in Friesland, numbers of staging Ruffs increased in the floodplains of the Pripyat River in Belarus, however. Here they were able to maintain high refueling rates (Verkuil et al. 2012a). As we know from resightings of colour-marked birds that individuals can switch migratory route between years, alternatively using The Netherlands or Belarus as spring staging site, Verkuil et al. (2012a) suggested that the western Ruff population possibly made an eastwards shift which also corroborate the global redistribution of breeding Ruffs over western Siberia.

The decline of western Ruffs is also observable from the wintering grounds thanks to aerial counts performed since the 1970s over the floodplains of the Senegal and Niger Rivers and in Lake Tchad (Zwarts et al. 2009). The loss of wintering Ruffs was most noticeable in the Senegal River delta, an area which has been best monitored. The delta hosted over 200,000 Ruffs in 1992, 135.000 in 1997 (Triplet and Yésou, 1998) but only 30,000 in 2001; since then, numbers dropped again to not exceed 5000 individuals (Triplet et al. 2014). This loss in Senegal may be partly linked to the disappearance of staging Ruffs in The Netherlands as these two sites share a strong migratory connection (OAG Münster, 1989). Whether Ruffs wintering in Senegal are simply "gone" or moved elsewhere is, however, difficult to tell. Numbers of Ruffs in the Inner Niger Delta and at Lake Tchad fluctuated around 100,000 and 300,000 individuals, respectively. Overall, the current numbers of Ruffs remain far from estimations of over the million individuals in the early 1970s (see Zwarts et al. 2009). The decline of Ruffs in West Africa may only partly be the reflection of changing condition up north. Wintering Ruffs were strongly affected by containment of rivers by dams which has tremendously changed the dynamics and extent of the floodplains (Zwarts et al. 2009).

Monitoring East-Atlantic Ruffs from their main staging site in The Netherlands

Shorebirds are iconic features of the Frisian landscape. Their successive appearances in spring, summer and winter either as passage migrants, breeding or wintering birds, rhythmed the open pastureland and are embedded in local culture of egg collecting and catching. These traditions translate a deep attachment to the land and the birds, even though birds and eggs were used for consumption. Facing the obvious declines of meadowbird populations, Frisians learned to turn things around. Egg collecting stopped and Frisians continued to walk down grasslands, this time to mark and protect nests during mowing. Similarly, traditional catchers, the "wilsterflappers", continued to capture birds for ringing in cooperation with scientists (Jukema et al. 2001b). Since 2004, this joint effort to capture and subsequently resight colour-marked birds was maintained every spring and allowed to mark and follow more than 5000 Ruffs. A unique dataset, which also give a unique opportunity to get a grip on Ruffs, being notoriously difficult to access and study elsewhere on the flyway.

Our study area comprised the core staging area for East Atlantic Ruffs and lays along the eastern shore of Lake IJsselmeer, between the villages of Makkum (53°03.18'N, 05°25.48'E) in the north and Laaksum (52°50.59'N, 05°25.16'E) in the south (Fig. 1.3). It encompasses 10,000 ha of low laying tracks of land enclosed

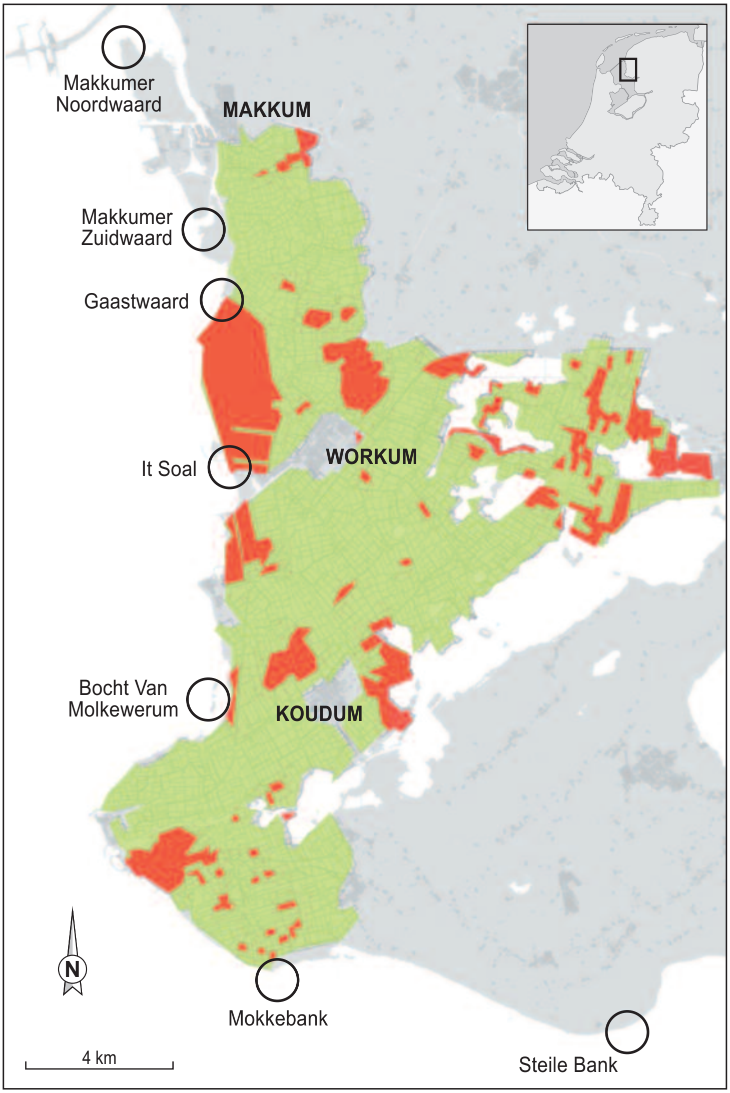

Figure 1.3: Map of the study area with vegetation typology (see Groen et al. 2012) and main night time roosts (black circles). Fields with "herb-rich" vegetation are indicated in red; fields with "herb-poor" vegetation are indicated in green.

by ditches and canals that traditionally offered herb-rich vegetation and high invertebrate availability due to the combination of high water table, soil type (clay, peat or sand) and a mild climate. However, the study area is now almost fully representative a modern Dutch agricultural landscape in which fields with monocultures of ryegrass (*Lolium* sp.) predominate (Groen et al. 2012). Three-quarters is covered by intensive grasslands, but also by arable land managed for the dairy industry, while the rest consists of the more traditionally managed fields, wet, flower-rich and often maintained as nature reserve.

Staging Ruffs feed actively in fields by probing the ground in search of earthworms and leatherjackets (van Rhijn, 1991; Beintema et al. 1995; Onrust et al. 2017, chapter 5) or pecking the above ground insects and typically rest during mid-day in inland wetlands scattered in the area (Verkuil and de Goeij, 2003; Schmaltz et al. 2016, chapter 4). At dusk, flocks get back to the IJsselmeer shores to roost during the night (Fig. 1.3), even though Ruffs might also be able to feed at night (Cramps & Simmons, 1983).

Our research group, in cooperation with the Frisian wilsternetters, caught and monitored staging Ruffs from early March, when the first males arrive on the study site, until mid-May when usually all Ruffs have left, the late arriving females too. Ruffs were caught during the day. Small flocks were attracted by adequate whistling and decoys placed on both side of the net laying in the grass. As birds are about to lend, catchers, hidden behind a screen about 20 m away, pulled the net using a rope while also helped by the wind (nets are called "wilsternets" and are equivalent to a 20 m long and 3 m high clap net; Piersma et al. 2005a). Catchers proceeded to metal ringed and biometric measurements before passing on the birds. In our hands, each individual was colour ringed applying a unique combination of 5 colour-rings on being a flag and then was aged, sexed and briefly described. Each day we looked for colour-marked birds in the field driving or biking along country roads across the study area. Observations were made by 5 to 6 observers with telescopes and thanks to the open landscape and dense network of roads, the study area was nearly completely covered every two days.

Outline of the thesis

Following extensive habitat deterioration and loss over the East-Atlantic flyway, western Ruffs migrate across a totally different landscape now than a few decades ago. In **chapter 2**, we first of all quantitatively re-assess the current non-breeding provenance and northward itineraries of the remnant population of Ruffs staging in The Netherlands. To do so, we explore the use of relatively cheap stable isotope ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{2}H$) measurements of different tissues to cost-effectively infer individual migratory patterns. We compared the multi-isotope patterns of feathers grown on wintering quarters, and of blood cells and plasma representative of staging areas and their habitats.

Chapter 3 aims at investigating Ruff adult survival which is likely an important determinant of population growth rate (Sæther and Bakke 2000) for shorebird species, like Ruffs, relatively long-lived with an early maturity but a highly variable recruitment due to the unpredictability of their breeding environments especially at high latitude. On the basis of our capture-resighting data, and using CMR models, we examined the year to year variation in apparent survival (i.e. mortality and permanent emigration are confounded) of male and females Ruffs staging in The Netherlands using the capture-mark-resighting data collected between 2004 and 2011. We also explored whether yearly variation in survival probability of Ruffs could be related to environmental conditions encountered on the flyway.

In **chapter 4**, we report changes in the foraging distribution of staging Ruffs in Friesland between spring 2006 and spring 2013 on the basis of resighting locations of our individually marked birds. We also repeated the transect survey of meadow use carried out in 2003 to compare habitat preferences of staging Ruffs 10 years apart.

In **chapter 5** we study how and when Ruffs detect and catch their earthworms prey in grassland. To do so we documented the daily changes in availability of surfacing earthworms in meadows used by Ruffs (during day and night) in their natural habitat and looked at their feeding performance in parallel. In a controlled indoor experiment, we examined which cues Ruffs are able to use during the day and at night to detect earthworms.

At last, in **chapter 6**, the general discussion, I summarize and reflect on what we learned on the decline of the East-Atlantic Ruff population in a decade of close monitoring of their main staging site in The Netherlands. I also provide an update on the spring staging performance of Ruffs since 2010. With the lessons learnt from this work, I will discuss the future path of research to study the Ruffs and other widespread inland species.