General discussion
Reasons for the decline of East-Atlantic Ruffs

Ruffs as breeding birds, and then as passage migrants, have declined in The Netherlands since the 1970s. In 2004, when the population monitoring of northward migrating Ruffs staging in Friesland started, the passage population of Ruffs was still counted in the tens of thousands, but two years later a sharp drop in numbers seemed to announce the imminent disappearance of the staging Ruffs (Fig. 6.1). It revived concerns and encouraged the first ecological work to elucidate the drivers of this loss, with the hope that knowledge would elicit solutions. The first evidence showed that the decreasing numbers of Ruffs using The Netherlands upon migration was linked with an eastward redistribution of the Arctic breeding population (Rakhimberdiev et al. 2010). The poor habitat quality of the Dutch intensive grasslands may have contributed to motivate a shift in the route taken by northward migrants, with a shift to more favourable eastern staging grounds (Verkuil et al. 2012a).

Since 2008 we have seen the declining trend in numbers slowing down and the numbers of Ruffs passing through Friesland stabilizing to around 5000 birds. By continuing the CMR monitoring, in this project we have tried to expand our knowledge on the decline of Ruff and bring more demographic and ecological evidence to the table. We also considered how the landscape has changed in Friesland, but also along the entire East-Atlantic flyway. In this General Discussion I will summarize our main findings and provide an update on the staging performances of staging Ruffs after 2008, with the aim to bring a broad reflection after a decade of Ruff research in Friesland.

Western Ruffs using a changing flyway

Wintering provenance and northwards itineraries of Ruffs staging in Friesland

In the course of the last few decades Ruffs of the East-Atlantic flyway have been faced with great changes of their environment, changes which certainly redistributed cost- and benefit- trade-offs along the way and influenced their contemporary migratory patterns. This thesis began with an examination of the current wintering provenance and northward itineraries for the remnant Ruffs that stage in Friesland during spring migration. At the population level, the connectivity links enabled us to identify critical sites and habitats, whereas the connectivity links at the individual level enabled us to examine how wintering origin and itineraries may be related to survival and reproductive output (e.g. for Black-tailed
Godwits see Kentie et al. 2017). The observational efforts outside our study site were too small to bring a quantitative assessment of the provenance and itineraries of Ruffs before they reach Friesland, and thus we could not rely on the resightings of colour-ringed Ruffs, and neither could we use satellite tracking devices which were still too large (and too expensive) to be applied on Ruffs. Therefore, we turned to isotope techniques for a cost-effective opportunity to address this question.

On the basis of multi-isotopic measurements ($\delta^{13}C$, $\delta^{15}N$ and $\delta^2H$) in their 9th primary feather (P9) grown on wintering site, we showed that most Ruffs staging in Friesland currently winter in sub-Saharan West Africa (75%, n = 149, ...

![Graph showing peak numbers of Ruffs from bi-monthly roost counts census](image)

**Figure 6.1:** Peak numbers of Ruffs from bi-monthly roost counts census (Meetnet Slaapplaatsen, Sovon/Centraal Bureau voor de Statistiek & Netwerk Ecologische Monitoring) over our study area from March to mid-May (black line). The grey line shows the estimates of the total spring staging population corrected for turnover rates (see methodological notes in the inset).

**Methodological note:** Staging population size estimates between 2006 and 2013 were based on the method of Frederiksen et al. (2001):

$$\hat{N} = n_1 + \sum_{i=2}^{k} (n_i - n_{i-1}) \varphi_{i-1}$$

where $\hat{N}$ is the total number of birds using the study site, k is the number of occasions (i.e. 6 bi-monthly counts), $n_i$ is the count at occasion i (1,2, ... k), $\varphi_i$ is the stopover persistence probability from occasion i to i+1 (i.e. Bi-monthly “local survival/staying” probability estimated by the CMR model of Cormack-Jolly-Seber –, Lebreton 1992 – we assumed that no mortality occurs during the migration period of Ruffs).
\[ n_{\text{total}} = 199 \]. Staging males that winter north of the Sahara represented a small proportion of our sample (15%, \( n = 29, n_{\text{total}} = 199 \)), which is nevertheless important considering that their proportion in the overall population is thought to not exceed a few percent (Chapter 2, Schmaltz et al. 2017). The European Ruffs were (as expected) associated with agricultural areas during the winter, at least for foraging, before they reached our study site. For sub-Saharan wintering Ruffs we showed that they probably occupied wetlands subjected to the influence of livestock, which could indicate that they mainly use the Inner Niger Delta in Mali where pastoral activities are important. \( \delta^{13}\text{C} \) and \( \delta^{15}\text{N} \) ratio measurements in blood cells and plasma indicated that sub-Saharan Ruffs, when spring migration begins, switch to the use of natural wetlands in the Mediterranean region, or possibly to rice fields either north or south of the Sahara. After that, they move to agricultural areas in Europe even before their arrival on the Frisian study site. This means that Ruffs on their way to Friesland, rather than regularly performing the previously suggested non-stop flights from Sub-Saharan wintering quarters (Jukema et al. 2001a; OAG Münster, 1998), move north in ways that depend on the availability and suitability of both natural wetlands and wet agricultural habitats (Chapter 2, Schmaltz et al. 2017),

**Changes over wetlands**

More and more western Ruffs (i.e. Ruffs following an East-Atlantic migratory route and staging in Friesland) have become limited to the use of man-made wetlands, including agricultural wetlands. Ricefields expanding over the Mediterranean Basin can provide suitable habitat for waterbirds as long as post-harvest management and flooding regime are appropriate (Sánchez-Guzmán et al. 2007; Navedo et al. 2015; Pernollet et al. 2015). It is known that during spring migration Ruffs use ricefield areas in southern Spain (Hortas and Masero, 2012), and in Italy (Bacetti et al. 1998), and this is what our isotope data suggested. Nevertheless, it remains to be understood whether rice fields can really ecologically replace the former natural wetland habitats. Is the presence of Ruffs in early spring in southern Europe linked to the changing habitat conditions in sub-Saharan Africa?

The containment of the Senegal river by the conversion of its delta into a vast irrigated zone dedicated to agriculture, and notably to rice, has been largely detrimental for Palearctic migrant waterbirds (Zwarts et al. 2009), including Ruffs. Originally numbering in the 100s of thousands, today only a few thousand Ruffs are wintering in the Senegal River delta, restricted to protected areas where floods are maintained artificially (Triplet et al. 2014). The loss of natural flood dynamics may be a threat too in the Inner Niger Delta, where flood extent are
reduced by the control the Niger River (Zwarts et al. 2009). The fluctuations in the global flood extent over sub-Saharan floodplains often tightly correlate with breeding population sizes of many Palearctic migratory species, including Ruffs (Zwarts et al. 2009). Lower flood extent limits foraging habitats available to wintering Ruffs that feed along and nearby the receding water lines, but lower floods also exacerbate hunting pressure on Ruffs and other waterbirds. Hunting occurs during the last stretch of pre-migratory fattening period of Ruffs, when the flood is almost fully recessed and birds are easy to catch as they tend to gather in the left-over waterbodies (Zwarts et al. 2009). Each winter, 10 to 40 thousand Ruffs are killed. Critically, the hunted Ruffs may be mostly females, the sex departing later than males especially during dry years when open waterbodies shrink most rapidly (Zwarts et al. 2009).

A possible selective loss of females

Over the last 20 years, spring after spring wilsterflappers in Friesland caught fewer and fewer Ruffs during migration and especially fewer females (Schmaltz et al. 2015, Chapter 3). The presence of females in Friesland became nearly anecdotal, often now limited to one flock of a few hundred during the last week of the passage. The fate of females certainly deserves attention. We observed and caught fewer females, but we also found that their annual apparent survival rates (i.e. product of true survival and fidelity) were lower than males during the springs of 2004 to 2011, which is unexpected for a polygynous species (Schmaltz et al. 2015, Chapter 3). This was true for birds which were most regularly observed on our study site every spring and thus rather site-faithful (i.e. birds with a high probability of detection). For such site-faithful birds, apparent survival estimates, are more likely to come closer to true survival rates.

At this stage, rather than conclude that these associations reflect causal relationships, we can only alert to the possibility that hunting in the Sahel, low female survival, and their disappearance from Friesland have something to do with each other. Not only may Reeves be prone to be shot in Africa, they also appeared more vulnerable to the intensification of the agricultural landscape and wetlands drainage over Europe (Verkuil and de Goeij, 2003; see also below). Also, , considering that Ruffs are lek breeders, from a dynamic perspective selective loss of females will greatly affect the presence of what is mostly a male-biased staging population. Recently, it was shown that male Pectoral Sandpipers (Calidris melanotos), another polygynous sandpiper species, nomadically sampled the entire breeding range, adapting their itineraries (i.e. tenure in each area) according to the local availability of fertile females (Kempenaers and Valcu, 2017, see also Lanctot and Weatherbread, 1997). Recovery data for Ruffs indicate that
females passing through Friesland are likely to end up in Scandinavian breeding areas (Zwarts et al. 2009), a region where breeding Ruffs declined more substantially than areas further east (Väisänen et al. 2005; Øien and Aarvak 2010; Lindström and Green 2013). A selective loss of females in the West could thus have contributed to encourage male movements towards the east of the range and Western Siberia, and thereby possibly the use of more easterly migratory route (Rakhimberdiev et al. 2011). Such circumstances could lead to local extinctions (Lee et al. 2011). This is only speculative, but emphasizes that the particularities of the mating system of a species must be kept in mind when trying to understand the responses of populations to global changes (Rowe and Hutchings, 2003).

Changes in Southwest Friesland

An evolving landscape

Already in 2001 our study area was largely occupied by a uniform and intensive agricultural landscape (Groen et al. 2012) which would have profoundly influenced the abundance, richness and availability of invertebrates for meadow birds, above and below ground (Vickery et al. 2001, Onrust, 2017). A steady decline in fuelling performances has been suggested to be a likely driver of the decline of Ruffs in Friesland (Verkuil et al. 2012). Unfortunately, comprehensive data to track the contemporary changes of agricultural practices and their impacts over the years have not been compiled.

Nevertheless, it was proposed that advanced application of manure on land could have contributed to reduce food availability for staging Ruffs (Verkuil et al. 2012a). Indeed, farmers have tended to manure their land using pipes to connect their tractor to a manure storage instead of directly pulling a storage tank itself onto the land. This lighter set-up permitted an earlier access onto the soft soil of lands to spread manure (i.e. allowed by laws from February 1st onwards). As for Ruffs, the application of manure created a temporary food peak of a few days, but then compromised invertebrate availability for several weeks. Earlier manuring meant that Ruffs arriving in March were miss-matched with “manure food peaks” and had to cope with a period of low food availability, but also with early and rapid growth of vegetation compromising further foraging opportunity later in the season (Verkuil et al. 2012a).

Therefore, in parallel to the work of chapter 4, we had also looked back at the date of manuring in farms of our study area. We consulted farmers and several “loondrijven” but there was no tangible evidence of earlier land manuring. The interdiction to manure before 1 February since the European Union Nitrates
Directive in 1991 constituted the biggest constraint and not all the farmers invested in lighter equipment. The timing of manuring is mostly dictated by weather and individual farm management. However, after 1991, several directives succeeded each other to regulate nutrients input and output of farms in the environment, which have globally stimulated the growth of milk production per cow and discourage pasture grazing (Ondersteijn et al. 2003). More ungrazed pastures would proportionally reduce the foraging opportunities of staging Ruffs even more given that Ruffs are unable to forage in the dense long rye-grass. Undoubtedly, the landscape is changing more than we think or see at first sight. I conclude that we should endeavour to better track the habitat changes brought about by farm management and legislations so that this essential background knowledge is available and serve future work on the stopover ecology farmland birds in Friesland.

Our attention turned on the attempts of environmental policies to mitigate the impact of intensive management on meadow bird populations. In south-west Friesland, agri-environmental scheme (AES) were mostly designed to counteract the decline of breeding species and much less targeted on the relations between habitats and passage migrants. Nevertheless, one of these measures marked a noticeable landscape change for Ruffs. We assisted to the rise of initiatives by farmers, but also nature organizations, to create shallow wet areas called “plas-dras” side-by-side to the intensive landscape. In such “plas-dras” areas one or several parcels are flooded between mid-February and mid-June to create shallow water available to the birds. They are a much more inclusive measure than most AES. Bringing back water on land immediately promote open and rich vegetation, a slower grass growth and thus later mowing, providing the original habitat features birds need to rest, forage and breed (Wetering et al. 2014).

Transect surveys made in 2003 (Verkuil and de Goeij, 2003), and again 10 years later in 2013 (Chapter 4, Schmaltz et al. 2016), established the importance of wet areas for Ruffs during the day. Indeed, we regularly observed flocks of Ruffs resting and bathing at mid-day. Ruffs also used these wet areas and their vicinity to forage, especially as the season progress and temperature warms. In fact, females, which arrive late, are particularly using them, as well as, the wettest grasslands (Verkuil and de Goeij, 2003); females rarely forage on intensive grasslands unless freshly mown or manured when they can benefit from temporary and easy access to invertebrates (pers. obs.). The presence of females in wet areas may in turn attract males which also use them to display, especially at the end of the passage period.

We showed that staging Ruffs initially foraging over polders along the coast of lake IJsselmeer have progressively retreated in the center of our study area and further inland, where precisely most of these artificial and temporary inland wet-
lands were established, especially after 2011 (Fig. 4.2; Chapter 4). Some of those wetlands were newly created, others already existed but were improved through management by nature organizations that cleared overgrown vegetation and reshaped shallow waters with mudflats edges. In parallel, the creation of the extended plas-dras of Pikesyl in 2011, northeast of the village of Oudega, and thus slightly out of our core observation area, has certainly also contributed to attract greater numbers of Ruffs. In recent years the number of Ruffs roosting there at night and close by increase while the number of Ruffs counted along the IJsselmeer shores tend to decrease (Fig. 6.2, A, B, see also Hornman et al. 2016).

*En route*, the greatest densities of migrants are found at times and in places where food is plentiful (Newton, 2006). Verkuil et al. (2012) hypothesized that re-creating wet grasslands areas could bring back the Ruffs in Friesland. If, within a single generation, Ruffs could move east to find more favourable staging habitats, they should as well be able to return west when conditions and especially food availability there would improve again. It is too early to say whether this happens or not. We showed that Ruffs responded promptly and positively to the implementation of wet areas in the landscape (Chapter 4), but it remains to be investigated whether the re-establishment of wet areas could effectively improve habitat conditions and food availability for staging Ruffs. Besides, whether or not south-west Friesland will be able to host again greater numbers of Ruffs in the future, as we have seen also depends on the protection of sub-Saharan floodplains and the persistence of suitable breeding conditions further north and east. In the period from 2009 to 2013, the decline in numbers slowed down and the remaining Ruffs retreated near wet areas (Fig. 6.1). I will now examine how staging Ruffs continued to perform from 2008 onwards. To do so, I estimated the average fuelling rate of staging Ruffs, adding data of spring 2009 to spring 2013 to update the analysis by Verkuil et al. (2012). Because birds were very rarely captured twice, we estimated the daily body mass gains from the slope of the generalized least square regression of the body mass of birds on their captured date adjusted for yearly and local variations in overall timing of migration (see Verkuil et al. 2012a for statistical details). However, as arrivals and departures of birds are often non-synchronized, it is only an approximate measure possibly underestimating the true fuelling rates of Ruffs (see Piersma et al. 2005b; Minias and Kaczmarek 2013).

We compared the population wide daily body mass gains between years from 2001 to 2013. Whenever fuelling conditions are limiting, birds may delay departure, or in contrast, choose to by-pass the staging site and use alternative staging areas. Therefore, we explore in parallel the variation in the spring staging duration of Ruffs from 2006 to 2013. As an exploratory exercise, we estimate the average minimal staging duration of adult male Ruffs in each spring from 2006 to
Figure 6.2: (A) Map of our study area, showing the core observation area (blue), the roosts along the IJsselmeer coast (orange circles) and the roosts in the Oudegaasterbrekken and Fluessen areas (green circles) used by Ruffs at night-time (counted by Sovon as part of the bi-monthly roost counts census Meetnet Slaapplaatsen, Sovon/Centraal Bureau voor de Statistiek & Netwerk Ecologische Monitoring). The empty circles indicate inland wetlands available to Ruffs in 2013 which they used to forage and roost during day-time (B) Peak roost count data among roosts of the IJsselmeer coast (in orange) and of the Oudegaasterbrekken and Fluessen areas (in green) from 2011 onwards (based on the coordinated counts of Sovon), (C) grey dots: Roosting sites available to the birds including all inland wetlands and night-time roosts, gray shading: resightings of colour-ringed Ruffs in 2008 and 2013 per polder unit. Numbers of sightings per polder unit are represented using a grey scale (see Fig. 4.2 in chapter 4 for details).

2013. This is the number of days between the first and last sighting of each birds resighted at least twice. We selected already-ringed males because catching and handling could affect birds, and increase their staging duration (but see Verkuil et al. 2010). Too few females were resighted twice within the same season to perform a similar analysis.

After 2008, we observed that similarly to the trajectory of numbers, the daily body mass increase for staging Ruffs continued to decrease slightly over years. It eventually leveled off for adult males which fuelled at relatively low rates of
between 0.48 g day$^{-1}$ (2011) and 0.75 g day$^{-1}$ (2013), compared with the daily mass gain of Ruffs staging in Friesland during earlier years but also of Ruffs staging in Belarus that increased at a stable rate of around ca. 1.2 g day$^{-1}$ (Verkuil et al. 2012a). Young males appeared to fuel less effectively than adults. For females, numbers were low and negative slopes may be related to asynchronous arrivals rather than because of females losing weight on the study site (Fig. 6.4A).

As for staging duration, overall years from 2006 to 2013 male Ruffs stayed on average a minimum of 17.8 ± 12 (SD) days in Friesland (n = 1428) and females slightly shorter 16.1 ± 13 (SD) days (n = 37). There were significant differences in mean minimal staging duration between years (KW test, Chi2 = 29.9, df = 7, P < 0.001), among which I denote longer staging duration in spring 2011 and spring 2012 (i.e. for both years, 20 days ± 12 (SD)) in comparison with earlier springs in 2006 (16.1 days ± 11 (SD)), 2007 (15.4 days ± 11 (SD)) and 2009 (16.5 days ± 11 (SD)).

There are several non-mutually exclusive explanations for the continuing decrease in daily body mass gain among males Ruffs. As we mentioned before, modern management of grasslands may continue to limit food availability for
males Ruffs. It may translate into a global decline of the fuelling rate of Ruffs, and/or it may be linked to changes in the behaviour or the occurrence of particular cohort(s) with different phenology and/or fuelling strategies (e.g. the earlier departure or disappearance of birds refuelling rapidly and/or becoming the heaviest). It may be modulated by local weather conditions.

Figure 6.4: (A) Population wide daily body mass gain in g day$^{-1}$ from captured Ruffs in South-west Friesland during spring passage migration period of 2001 to 2013. (B) Mean minimal staging time from the resightings of previously ringed males (2006–2013) in function of population wide daily body mass gain (g day$^{-1}$) among adult males captured in the respective year.

With five more years of data at hand than Verkuil et al (2012), we found no tendency for an extended length of stay among males Ruffs that would allow (and explain) an overall lower refuelling rate and sufficient departure weight. Neither did we confirm the suggested tendency for the decrease in staging duration. Our
results suggest that yearly variation in minimal staging duration relate to the population average fuelling rates (among adult males Ruffs - $F_{1.6} = 9.263$, $P = 0.02$, $y = -7.56 \times + 22.5$, $R^2 = 0.61$). Adult male Ruffs may only be able to adjust their staging time (determined by fuelling conditions in Friesland), by slightly extending their stay during years when average fuelling rates were lower (Fig. 6.4B).

Nevertheless, to learn more the stopover dynamics of Ruffs, I recommend that our dataset is re-analyzed with the newest and promising CMR methods. This would allow a stronger inference based on improved staging duration estimates (i.e. considering that the individual retention probability at a specific site will depend upon the time already spent there) and opening the opportunity to investigate the relationship between fuelling conditions and length of stay, and explore inter-individual differences (i.e. sexes, age, wintering origin - Guérin et al. 2017).

Clearly, we also need to learn more in the future on how the management of meadows is influencing the availability of invertebrates for staging Ruffs. Ruffs are thought to refuel mainly on soil dwelling invertebrates, earthworms (Lumbricidae – van Rhijn, 1991) and leatherjacket larvae (Tipulidae – Beintema et al. 1995). Ruffs could use their hearing to catch abundant earthworms surfacing at night, but they showed to be diurnal feeders (Onrust et al. 2017 - Chapter 5). During indoor experiments, we showed that Ruffs mainly use visual cues to detect worms during the day, such as burrows or fresh casts of earthworms remaining close to the surface (Onrust et al. 2017 - Chapter 5). While it may still be more advantageous for Ruffs to forage during the day, the lowering of water table as part of intensive management practices implies a less penetrable soil for probing Ruffs and forces earthworms to retreat deeper in the soil to find moist conditions. Intensive management thereby favours earthworm species that live in deep vertical burrows during the day and challenge the ones remaining in the top soil. The work of my colleague Jeroen Onrust (2017) on the availability and abundance of earthworm species for shorebirds in relation to management practices in Friesland shed light on the determinants of food availability for shorebirds, and fuelling Ruffs upon migration.

At this point we should not forget that Ruffs also hunt insects, especially towards the end of the passage period. First the wet and mild weather of March maintains short grass, and a soft and penetrable soil for Ruffs probing for soil-dwelling invertebrates. However, when temperature increase in the course of April, the soils dry up and the grass grows rapidly, Ruffs shift to most extensive meadows, wet areas or seize opportunities to feed onto freshly mown intensive meadows. This is when we consistently observed Ruffs changing their foraging behaviour to pecking insects instead of probing the soil (Fig. 6.5). The only
exception was during spring 2013, an exceptionally late and cold spring, perhaps allowing Ruffs to probe prey in the soil until late in the season.

Again, drainage, repeated mowing, high input of fertilizers, lack of livestock grazing and the use of pesticides may well have influenced the abundance and communities of insects in the grasslands in Friesland and thus their availability to meadow birds and their chicks (Vickery et al. 2001; Devereux et al. 2004; Hallman et al. 2014, 2017). It was shown, for instance, that chicks of Black-tailed Godwit using intensive fields in Friesland had lower feeding success (Schekkerman and Beintema, 2007), but also a slower growth and lower subsequent survival
(Kentie et al. 2013) than chicks living in herb-rich grasslands. In comparison, nothing is known on the influence of intensive practices on the availability of insects for refuelling Ruffs in late April and early May, right before their departure to the breeding grounds.

Clearly, there is much more work to be done in order to understand the foraging and fuelling strategies of Ruffs during their stay in Friesland. I would recommend including seasonal aspects within the migration period of Ruffs, such as changes in habitat use, foraging behaviour and prey choice of staging Ruffs but also look at the influence of local weather.

Fitness repercussions of a deteriorating staging site

Friesland is thought to be the last staging area of Ruffs before heading to breeding grounds, and thus the last opportunity to accumulate the necessary energy to migrate and initiate breeding, starting with the ‘lekking’ of males. The deteriorated habitat quality of key staging site like Friesland may have contributed to motivate large scale emigration of birds towards Eastern Europe and among other via the floodplain of the Pripyat in Belarus (Verkuil et al. 2012a). However, for the individuals faithful to the western route, sub-optimal fuel storage could certainly involve subsequent fitness costs.

Our survival analysis showed that amongst the Ruffs most reliant to Friesland, i.e. those with a high detection probability on the staging site every year, the sexes differed in survival. Looking back over the period 2004–2008 when mark loss was not yet a problem, the average annual apparent survival probability of highly detectable females was low ($\hat{\phi}_\text{2004-08} = 0.64$, range 0.57 – 0.81). In contrast, the average annual apparent survival probability of highly detectable males was clearly higher ($\hat{\phi}_\text{2004-08} = 0.85$, range 0.81 – 0.93), which is in line with an expected survival rate of 0.8 for birds living on average 4 to 5 years (Seber, 1982; Schueller and Stiefel, 1985). This suggests that true survival may really have been very low for the site-faithful females. This could relate to a possibly female-biased increase in the hunting pressure at the sub-Saharan wintering grounds, but the quality of the staging site in Friesland could also contribute differentially more for the smaller and later females.

If not influencing survival, sub-optimal fuel stores upon departure from Friesland could also carry-over to the males’ subsequent breeding efforts. These males may be able to forage enough during the breeding season in order to survive (Lesku et al. 2012), but compromise feeding may translate into lower quality of ornaments, lower endurance to sustain lekking activity, fighting rivals and courting females (Kempeneers and Valcu 2017). As a result such males would be less competitive and have less access to mating than males using more eastern staging areas and flyways with whom they share the breeding grounds in most northern Scandinavia and western Russia regions. This would then contribute to
exacerbate an unbalanced breeding output between the parts of the population migrating along eastern and western flyways. Although this is purely speculative, the decline of Ruffs along the East-Atlantic route could be the result of many intricate processes and of ecological drivers much of their enormous range.

**Heterogeneity in the use of Friesland**

Ruffs are well known for their elusive nature, a feature which makes them both exciting and difficult to study. In sub-Saharan Africa, Ruffs are difficult to study and the Dutch Ruffs here disappear among the large numbers from elsewhere. The breeding grounds, being so vast, offer no better options to monitor Ruffs. Adding insult to injury, Ruffs may display nomadic breeding movements.

Thus, studies on staging sites really represent an opportunity. Major staging sites on the flyway of migratory birds like Friesland are few and therefore channel all kinds of individuals, from different origins and destinations, with variable staging behaviour, and probably each with a fitness profile associated with their own strategy. This heterogeneity in their use of Friesland was clearly apparent, and challenged the interpretations of the data. At the same time this heterogeneity carries great potential in terms of ‘hidden’ underlying information from an entire flyway. Efforts to indirectly characterize our marked individuals (e.g. short versus long distance migrants, migratory connections or fidelity patterns) would open a great comparative power to investigate migratory behaviour in an evolutionary context and to better understand population dynamics.

On the basis of our capture-resight data of males during spring 2006 to 2013, we indeed observed nonsynchronous arrival and departure dynamics among staging Ruffs using Friesland. Capture mark-resight models (Lebreton et al. 1992), enabled us to estimate a stopover persistence probability ($\varphi$ – i.e. probability to stay on the staging site – Schaub et al. 2001) to quantify departures ($(1 - \varphi)$ being the probability to emigrate) and a probability to immigrate ($1 - \gamma$ (seniority) – i.e. probability to arrive on the staging site - Pradel, 1996, Schaub et al. 2001) modelling arrivals during the spring migratory period (i.e. March 1 and May 15 – see Fig. 6.6 for details of methods). We see that mid-March marked the peak of arrivals, with arrival continuing until the end of the month. A low but steady immigration probability until 20 April, however, suggested that some birds continue to arrive until late in the season (Fig. 6.6). In parallel, most departures occurred from 20 April when the stopover persistence really dropped, but there could be some earlier departures already in the beginning of April (Fig. 6.6). This provides evidence that arrivals and departures probably spread over two to three weeks at both end of the migration period.
Figure 6.6: In grey, the estimated staging persistence probability ($q$) of Ruffs in Southwest Friesland over the period 2006–2013, from best ranked model ($q$ (date) $p$(date x year)). In black, the estimated immigration probability ($1 - \gamma$ (seniority)) from best ranked model ($\gamma$ (date) $p$(date x year)). In both cases, error bars indicate 95% confidence intervals.

**Methodological note:** Our calculation are based on resighting histories of previously ringed adult males (see Verkuil et al. 2010) captured and observed on our study site, set by 5 days periods (i.e. 15 “sampling” occasions). The stopover persistence probability ($q$) is a local survival probability giving the probability that a ruff present on the study area “survive” or stay between two consecutive time intervals. The immigration probability ($1 - \gamma$) is the reverse of a seniority probability ($\gamma$): the probability that an individual was already on the staging site before the current observation period (Pradel, 1996, Schaub et al. 2001). It is equivalent to a survival analysis running backward in time. For each case, a resighting probability ($p$), estimated simultaneously, account for imperfect detection. To be able to describe movements in and out of our study site and over years, each parameter could vary in function of years, date (5 days periods) and the interaction of year and date. This way we compared a set of 4 models for stopover persistence and seniority probabilities.

Best ranked models, according to Akaike’s Information Criterion, were: $q$ (date) $p$(date x years) and $\gamma$ (date) $p$(date x years).

In parallel, we found indications of heterogeneous use of Friesland reflected by heterogeneous year to year detection probability among marked Ruffs. This could be arise from individuals showing different fidelities to Friesland, and/or residency time (i.e. staging duration). There were light birds among late captures into the migratory passage period which brought another evidence for spread arrivals.
So far, we handled this diverse “staging phenology” with statistics to reduce biases during our analysis as we first considered the staging population as a whole. However, reflecting on the ‘average’ of a population eventually has limited interest. Instead, finding ways to characterize variability in staging behaviour and migratory connectivity at the individual level would be a prerequisite for stronger inference.

In the field, Jukema et al. (2001a) already suggested that spread arrivals onto the staging site could partly be explained by the first arrival of males wintering in Europe in late February followed by later arrival in the second half of March by Ruffs returning from sub-Saharan Africa. The late February arrivals do not seem to occur anymore and we found no evidence for the first occurrence of male Ruffs assigned to European wintering quarters with feather’ stable isotopes among catches during spring 2012 (Chapter 2). Yet, gathering our resighting data obtained during the winter time in Europe, the suggestion of Jukema et al. (2001a) is borne out with European males arriving first in Friesland and also tend to stage longer than their African counterparts (Fig. 6.7 and 6.8).

During the winter, Ruffs colour-ringed in The Netherlands were sometimes resighted by observers in The Netherlands, Belgium or the United Kingdom, in Spain or Portugal, but unfortunately almost never in Africa. Assuming that Ruffs were faithful to their wintering quarters, we considered a bird as wintering in Europe if it was seen, in any year, north of the Sahara between October and December. Several individuals were observed repeatedly in Europe over years despite the low observation effort. We examined the phenology of these European males in the staging site in Friesland by calculating the cumulative percentage of first and last sightings from these “European males” during each spring migratory period (March 1 and May 20), from 2006 to 2013. To compare we performed the same analysis for males that were never observed during the winter and for females (Fig. 6.7). We also test for differences between the average minimal spring staging duration (i.e. number of days between first and the last sightings of individuals observed at least twice during migration) of “European” and “unknown” males (Fig. 6.8). Females, in low numbers and rarely observed twice in a same spring season, were not considered.

On the basis of our resighting data we indeed observed that European Ruffs were arriving first, followed by the rest of the males with unknown wintering origin but yet most probably in a strong majority coming from Africa. Females arrived last as usually described (Fig. 6.7A). In contrast, the departure of all birds appears rather synchronized and may indicate that all may use similar cues to leave the staging site. The earlier arrival of European males while their departure is synchronized with others led us to expect a longer staging duration in Friesland. And, indeed, we observed a consistent tendency of European males to stay
Figure 6.7: Mean cumulative percentage of (A) first and (B) last sightings of previously colour ringed Ruffs over spring 2006 to 2013. The lines indicate mean values; standard errors are represented by the shaded areas. Blue: males that have been seen at least once in Europe during winter (October to December), Green: males of unknown wintering origin, Red: females. The grey lines alternatively represent the mean cumulative percentage of first (in plot B) and last sightings (in plot A) to facilitate comparison between arrival and departure patterns in each plot.

longer relatively to the males of unknown wintering origin (Fig. 6.8) yet the difference was only significant in 2009 (KW test, Chi² = 4.75, df = 1, P = 0.02) with European males having a minimal staging duration of 21.5 days in Friesland compared with 15.6 days for the rest of the staging males.

This example suggests that males with different wintering distributions employ different staging strategies upon northward migration. This means that the impact of deteriorating conditions on the staging site may very well differ according to the staging strategies employed by these birds.
Figure 6.8: Minimal staging duration of Ruffs in Southwest-Friesland during spring migration 2006 to 2013. Dark grey: Males that wintered in Europe, light grey: males with unknown wintering quarters. In each boxplot, the middle horizontal line represent the median values, the lower and upper hinges correspond to the first and third quartiles.

Concluding remarks

We aimed to monitor and detect changes in abundance, annual survival and behaviour of Ruffs staging in southwest Friesland during northward migration, with the intention to better understand the factors and mechanisms driving the overall decline of Ruffs along the western flyway, the East-Atlantic Flyway.

We reported the decrease in peak numbers of staging Ruffs roosting in southwest Friesland from 2008 to 2013, followed by a slight increase in numbers in 2014 and 2015 (Meetnet Slaapplaatsen, Sovon/Centraal Bureau voor de Statistiek & Netwerk Ecologische Monitoring). In parallel, the numbers of Ruffs caught by Wilsterflappers in the field also decreased until 2013 (i.e. last year of the monitoring effort) and notably a stronger diminution in the proportion of females.

We analysed apparent annual survival patterns of males and females separately based on individually colour marked individuals between 2004 and 2011. From our analyses it is clear that the study population is not closed, and made of individuals probably using the staging site differently in terms of fidelity and/or...
residency time. Without resighting data from outside our study area to estimate Ruffs’ fidelity to Friesland, we cannot unambiguously estimate a true survival rate. Yet, using multievent CMR models we could model an apparent survival probability from birds sharing a high detection probability and hence more prone to use Friesland. It provided us with closer estimates of the ‘true’ survival, and showed that male survival was estimated close to what would be expected for the species, while for females estimates of survival were consistently lower suggesting a difference in habitat use, migratory behavior or real survival between the sexes, and thus a potential difference in the habitat demands and therefore protective measures.

Low female survival is consistent with sex-biased hunting pressure in the Sahel and could be one driver of the loss of females. On the staging site, females showed the greatest preference from the traditional and extensive grasslands habitat and wet areas, and therefore drainage and loss of inland wetlands in Friesland could be another important factor in the loss of females locally.

Males Ruffs staging in Friesland during spring migration show variable wintering grounds. The early males wintered more in Europe, followed by males wintering more in the Sahel. Males wintering in Europe were in the minority. Nevertheless, with respect to the numbers of Ruffs estimated to winter in Africa and Europe, Friesland is a very important staging area. Most staging birds are wintering in sub-Saharan floodplains of the Sahel. Our work suggests that during migration, rather than performing a single non-stop flight, these sub-Saharan Ruffs move northward in a stepwise fashion, probably according to the availability of suitable wetlands and agricultural areas until they reach Friesland. We ignored whether this is a new pattern or not, and how much the ongoing deterioration and conversion of natural freshwater wetlands have been influencing the northward itineraries of Ruffs so far.

This project also showed the isotopic complexity of habitats used by Ruffs, starting with sub-Saharan wetlands subjected to high evaporation and anthropogenic influences. We hope that in the future we will be able to collect more ground-truthed isotopic samples and couple this data to the tracks of individuals equipped with satellite tags to assess the reliability of isotope technics to investigate migratory connections of Ruffs and other ground-foraging species closely associated to freshwater wetlands. We will then find out if our inferences were correct.

At the northern end of the migratory journey of Ruffs, we know nearly nothing about how Ruffs (i.e. males and females) make the transition to their breeding sites, and their breeding ecology in the wild. Such knowledge is essential and would enable to properly design the monitoring of Ruffs’ breeding output, an obligatory step if we are to understand the population dynamics of Ruffs.
The data collected in the course of the last decade in Friesland increased our knowledge, but are far too poor to really understand the cause and mechanisms behind the decline of Ruffs population in the East-Atlantic. One main challenge is to work on an (open) subsection of the Ruff population which is nearly panmictic, considering its genetic diversity and considerable exchanges over their large distribution range (Verkuil et al. 2012b). A second problem is the lack of knowledge on the reproduction and connectivity patterns to breeding sites.

The setting up of a thorough demographic monitoring for the Ruff population (i.e. breeding productivity, survival and movements) would demands extraordinary extended and coordinated efforts. As we speak, I would strongly recommend to make a step back and first invest in tracking devices to establish and to learn about the connectivity patterns of Ruffs worldwide, for males and females separately. Only then we shall be able to appreciate how the population function as a whole and design an adequate monitoring scheme. Small satellite tracking devices are now available on the market (Chan et al. 2014). In parallel to individual tracks, isotopes technics could be a precious to cost effectively assess migratory connections on greater numbers of individuals. Some more work merit to be done to examine the feasibility of geographical assignments based on multiple isotopes for Ruffs using different tissues and perhaps also using more isotopic elements.

Yet, knowledge on migratory connectivity worldwide does not mean that we are able to advice adequate protection measures. We will have to develop more ecological research on Ruffs in different parts of the flyway, to collect more knowledge on how habitat use and related aspects enhance the odds of both their survival and reproduction. Our best guess to protect Ruffs at the moment is to increase the extent of habitats frequently used (e.g. wet habitats in Friesland) and ban the hunting of waterbirds in sub-Saharan Africa floodplains. But there are no ready-made answers. Solutions are to be found beyond the concern for a particular species, or a particular group, or everyone’s best short-term interests. Solutions can only be global and in the interest of all players. We need sustainable land and water management that balance human needs with the preservation and restoration of the natural dynamics of our ecosystems. The task is enormous, almost impossible, yet essential to pursue if we are to preserve the world around us.