Individual and population-level evidence for a large-scale, within-generation shift in a shorebird migration route

Yvonne I. Verkuil, Natalia Karlionova, Eldar N. Rakhimberdiev, Joop Jukema, Jan J. Wijmenga, Jos C.E.W. Hooijmeijer, Pavel Pinchuk, Allan J. Baker & Theunis Piersma

In most migrant birds, young perform their first migration independently of adults. The presumed dearth of learning opportunities has been linked to a lack of fast adaptive change in migration routes. Here we describe the first example of an adaptive route change within a generation of a migratory bird. Ruffs (Philomachus pugnax) migrating from West Africa to Fennoscandinavia and Russia via The Netherlands, shifted to alternative staging areas, after staging performance was compromised. Between 2004-08, 4,363 males were tracked by individual colour-ringing and partly, by radio-tags. Between 2004-08, 145 individuals previously colour-ringed in The Netherlands occurred increasingly eastwards, as far as the next major staging site, 1500 km east in Belarus. This individual flexibility correlated with a new April cohort of 20,000 migrants appearing in Belarus. Capture-resighting methods revealed that individual length of stay of the Dutch migrants declined from 23 to 19 days between 2005-08. Population estimates adjusted for the length of stay corroborated the decline Dutch migrants by 15,000 individuals. The Dutch migrants declined twice as fast as the European breeding populations. From 2001-08, mass gain rates declined in The Netherlands, even when wintering ground conditions were accounted for statistically, whereas rates remained constant in Belarus; also the extent of ornament development in Dutch males decreased. Declines in various measures of staging performance (length of stay, body mass gain, ornament development) suggest that loss of habitat quality has induced the shift of migration routes eastwards. This indicates that shorebirds, counter to previous expectations, do show fast and adaptive changes in migration routes.
Introduction

In a changing world, migrant birds would benefit from a capacity to respond appropriately to sudden alterations of critical habitats (Both & Visser 2001; Baker et al. 2004; Piersma & Lindström 2004; Both et al. 2006; Piersma 2007; Pulido 2007). In his stimulating review of documented cases of adaptive change of migration routes, Sutherland (1992, 1998) suggested that species with cultural inheritance (i.e. where parents accompany their young during first migration) would be more plastic than species where young migrate independently (where an inherited program would steer the first southward migration). Indeed, even with strong directional selection, captive passerines required several generations to adapt to new migratory directions (Berthold et al. 1992). Within generation geographical shifts in migratory routes of birds are exclusively reported for long-lived species with extended parental care (Newton 2007; Bauer et al. 2008). In other species migratory behaviour is expected to be genetically controlled (Böhning-Gaese et al. 1998; Pulido 2007). Here we report the first example of a rapid change in migration routes in a species without extended parental care, the ruff (Philomachus pugnax, Linnaeus 1758, Scolopacidae). Ruffs are typical shorebirds in which most juveniles during first southward migration travel independently of adult birds (van Rhijn 1991); they are thus expected to be genetically constrained to fixed migration routes (Sutherland 1998).

Ruffs use inland wetlands, including agricultural landscapes with high water tables (Wymenga 1999; Zwarts et al. 2009). Physiological adaptations to long-distance flights (Piersma 1998; Vaillancourt & Weber 2007) enable their migrations between tropical wintering areas and arctic breeding sites. Wintering areas host ruffs of mixed breeding origin. For example, ruffs wintering in the Sahel breed between 10° E in Europe to 160° E in Russia (Zwarts et al. 2009). They segregate during migration: Siberian breeding birds use Eastern Europe during migration, where as the Western European flyway connects to the European Arctic but also to Western Siberia (Zwarts et al. 2009). Three major European staging sites, with over 10,000 ruffs, are recognized: (1) the agricultural fields of Fryslân (The Netherlands, Western Europe), (2) the floodplain meadows of the Pripyat river (Belarus, Eastern Europe), and further east, (3) the limans and agricultural fields of the Sivash (Crimea, Ukraine) (Chernichko et al. 1991; Jukema et al. 1995; Mongin & Pinchuk 1999; Wymenga 1999; Jukema et al. 2001; Karlionova et al. 2007). Females traditionally use easterly sites; in Fryslân they pass through in low numbers (Wymenga 1999). Ruffs are sexually dimorphic (but see Jukema & Piersma (2006)); the larger males develop their colourful sexual ornaments during staging on northward migration (Jukema & Piersma 2000). The combined activities of refueling, moulting and ornamentation elevates energetic requirements (Buehler & Piersma 2008) suggesting that ruffs require high quality staging habitats.

Ruffs in Fryslân have been in decline over the last decades, with spring numbers decreasing since the 1990s (Wymenga 2000; Zwarts et al. 2009; Delany et al. 2009). This reduction might reflect declining numbers of breeding birds or reflect shifts in distribution. Parallel studies in the closest western and eastern staging areas, Fryslân and
Pripyat, 1500 km eastwards, created a unique potential to examine whether ruffs are shifting spring staging sites. Local staging conditions in both areas were assessed from 2001 to 2010, by comparing population dynamics, migration phenology, refueling rates and development of sexual ornaments.

Methods

Counts, catches, colour-marking and radio-tagging
In Fryslân, the spring passage of ruffs was studied in a 400 km² area dominated by dairy farms (centred on 52°58’ N 05°24’ E). Until the late 1990s up to 60,000 ruffs passed through from March until May (Jukema et al. 1995; Jukema et al. 2001). Ruffs feed on grassland, and roost along the shallow shores of Lake IJsselmeer and smaller inland lakes (Verkuil & de Goeij 2003). Between 2001–2010 on dates close (± 3 days) to the 1st and 15th of the months of March-May, volunteers counted birds at the nine main roost sites (van der Burg & Poutsma 2000), covering the area used by staging ruffs. Since 2001, ruffs were captured with wind-driven clap nets, using a flock of decoys to lure flying birds in front of the net. Beginning in 2004, the Dutch migrants have been colour-marked and resighted annually, as part of the Global Flyway Network efforts to assess the demography and migration shorebirds worldwide (Piersma 2003, 2007).

Each captured ruff was given a numbered metal ring, a unique combination of four colour bands and a coloured ‘flag’. The birds were weighed to the nearest g. For sex determination wing length was measured with a stopped ruler. In ruffs discrete distributions of wing length are found for females (<170 mm) and ornamental males (>180 mm); non-ornamental males, so-called faeders (Jukema & Piersma 2006), occur in low frequencies (around 1%, Chapter 5) and are not considered here. Birds were aged by leg and plumage characteristics; until their second calendar year ruffs have green or spotted green legs, and buff wing coverts (Meissner & Ziêcik 2005; Meissner & Scebba 2005). The moult of the ruff feathers of ornamented males was scored in six classes, 0 being least developed, and 5 being most developed.

Between 25 March and 15 May 2004–2008, the study area was covered daily to check for colour-marked ruffs. Due to sample size constraints for the scarce females and faeders, only resighting data on ornamented males, hereafter called males, will be presented. For males, 7,550 resightings were collected, including multiple resightings of 4,363 individuals (between 744 and 1052 annually). Resightings probabilities varied between 0.11 and 0.17 for two-day intervals (Chapter 6). Resightings were used to generate estimates of individual length of stay (Chapter 6), and population size. In addition to local resightings, the general public provided 145 resightings of colour-ringed individuals from elsewhere in Europe.

To supplement observations of colour-marked birds, 48 and 47 ruffs were fitted with radio-transmitters in 2005 and 2007, respectively. Automatic receiving stations (ARTS) with a maximum range of 5 km were erected at the nine roosts, covering the
ARTS, from 25 March to 1 June, continuously sampled each individual at 20 min intervals for 20 s, with sample intervals of 5 s, at 40 pulses per min, thus collecting a maximum of four positive signals per 20 min. An individual was considered present if three out of four instances had signal to noise ratios larger than 1.5 (see Green et al. (2002); Rogers et al. (2006); van Gils et al. (2006)).

The Pripyat river flood plains (Belarus, Turov, Gomel Region; centred on 52°04’ N 27°44’ E) supports 10,000–40,000 ruffs annually between March and May (Mongin & Pinchuk 1999). From 2001 onward ruffs were caught on small islets (in total about 2 km²) in floodplain meadows, mainly with walk-in traps and occasionally with mist-nets. Each captured ruff was ringed with a numbered metal band, weighed to the nearest g and aged and sexed. Foraging and flying birds were counted along fixed routes. Transect counts were carried out 7 times in 2001, 23 in 2002, 18 in 2003, 34 in 2004, 48 in 2005, 50 in 2006, 64 in 2007, 75 times in 2008, 42 times in 2009 and 36 times in 2010. Presented data are cumulative numbers for each transect count. To enable comparison with the bi-monthly counts in Fryslân, the maximum count of each half month was used.

**Estimating passage population size and length of stay**

Following Frederiksen et al. (2001), the size of the passage population was estimated as:

\[ N_{\text{new, current}} = N_{\text{total, current}} - N_{\text{total, previous}} \times \phi_{\text{previous} \rightarrow \text{current}}, \]

where \( N_{\text{new, current}} \) is current number of new birds; \( N_{\text{total, current}} \) is total count in current time period; \( N_{\text{total, previous}} \) is total count during previous time period; \( \phi_{\text{previous} \rightarrow \text{current}} \) is local survival or staying probability from previous to current time period. Estimates for \( \phi \) were obtained from survival analyses (see below). Census data were collected bimonthly; hence a cumulative 14 d staying probability was calculated by multiplication of 2 d staying probability estimates. Staying probabilities for 1-24 March were set to 1, after backward extrapolation of later staying probabilities (Chapter 6). Estimated population size is the sum of \( N_{\text{new, current}} \) for all 14 d periods. Birds counted between 1-15 March were considered all new arrivals; as numbers in March were low this assumption did not markedly affect the grand total.

Staying probability (\( \phi \), probability to stay to \( t+1 \)), and seniority probability (\( \gamma \), probability to have been in the study area at \( t-1 \)) were modelled according to Schaub et al. (2001). With \( \phi \) duration of stay after encounter was estimated and with \( \gamma \) duration of stay before encounter, which add up to total length of stay (Schaub et al. 2001). To not violate the assumption of equal resighting probabilities for each time interval, only ruffs colour-ringed in a previous year were used to estimate length of stay (Chapter 6).

Encounter histories with 2-day intervals were generated, beginning on 25 March in the year after marking. This resulted in 113, 461, 451 and 437 encounter histories respectively in 2005, 2006, 2007 and 2008. Only 2 d time intervals with >9 resightings were used in the analyses (Morris et al. 2006; Gillings et al. 2009). This requirement was not met for most time intervals in 2005, so this year was excluded from the analyses.
Mark-recapture logit selection procedures according Pradel (1996) and White & Burnham (1999); (Chapter 6) were applied. Most parsimonious models were used to generate estimates for length of stay by bootstrapping following Schaub et al. (2001). Annual variation in estimates of length of stay were analysed with a linear model, with Year as categorical factor and Date as co-variable (SPSS 16).

For radio-tagged birds, minimal length of stay (time between day of tagging and last detection) was calculated (Warnock et al. 2004). Capture-recapture modelling did not apply as initial seasonal encounter was the capture occasion which violates the assumption of equal encounter probabilities for each time interval. To not underestimate length of stay, only birds tagged in the first two tagging cohorts (24-26 March and 1-2 April) were used (n = 20 in 2005; n = 22 in 2007).

**Modeling the rates of body mass increase and moult**

Refueling and moulting rates were used as a measure of local staging performance (Lindström 2003). Moult may be a relevant indicator of habitat quality, as it starts from zero at the staging site (Jukema & Piersma 2000). To account for a carry-over effect of wintering conditions on local staging performance, data on the flood extent of ruff habitats in The Sahel during the preceding winter were factored in. The inundation areas were taken from Zwarts et al. (2009), being 13,625 km² in winter 2000–01, 13,907 km² in 2001–02, 10,874 km² in 2002–03, 15,433 km² in 2003–04, 10,874 km² in 2004–05, 12,390 km² in 2005–06, 13,458 km² in 2006–07 and 14,602 km² in 2007–08.

To estimate the rates of body mass increase, the modeling approach of Zuur et al. (2009) was applied in ‘R’ (R Development Core Team 2008). The variation in body mass with date, year, sex, age, staging site and flood extent was modelled. To determine whether trends found in adult males apply to the total population, in these analyses males in their second-calendar year (2cy) and females were included.

First a general linear model of Bodymass was fitted with the variables Date, Year, Group (adult males, 2cy males, females), Place (Fryslân, Pripyat) and Wint_cond. Date was centred as follows: Date – (firstday(for each place and year)-lastday(for each place and year))/2) and converted to (centred date – min(centred date) + 1. The variable Year was treated as a continuous variable and transformed to Year-min(Year) +1. The variable Wint_cond (wintering conditions) was scaled by the “scale” R function. This general linear model yielded residuals that violated homogeneity assumptions: variance increased with Date (cone shaped pattern) and variances were different between groups. To deal with heterogeneity in variances, the generalized least squares (GLS) method (Pinheiro & Bates 1996; Pinheiro et al. 2008) was applied as follows. The initial model included Bodymass as response variable and explanatory variables Date, Year, Place, Group and Wint_cond and all their interactions, except between Year and Wint_cond. Residuals variances were modelled using GLS with Restricted Maximum Likelihood estimation (REML). The constant plus power of variance covariance function was used to model the variance structure (varConstPower(form=~Date | Group)) as it had the lowest AIC. There were no temporal autocorrelation patterns, so the random part of the model included only the variance structure. Next the model was refitted in
GLS using Maximum Likelihood estimation (ML) and reduced by backward selection of interactions. The same procedure was followed to model arrival body mass, using data of the first catch of each season. Heterogeneity of variance in Group was found and hence for the factor Group, the varIdent variance structure was applied. For final models with remaining interactions see Supporting Information.

To analyse moult patterns, the feather growth and advances into the next stage were assumed to be linear (Underhill & Zucchini 1988). The starting model was a maximal linear model (LM) including Stage as the response variable and all interaction terms between Sex, Year, Date, and a quadratic term of Date (date^2) as explanatory variables. Variables Year and Date were transformed as explained above. Heterogeneity in the LM model was detected; hence the model was refitted with the GLS method from the linear and non linear mixed effects models (nlme) R package. The optimal variance structure of the model was a combination of a constant plus power of the variance covariance structure of Date and Sex plus a exponential variance structure of Year (varComb((varConstPower(form=~cDate|Sex), varExp(form=~pos Year))). Temporal autocorrelation was not significant. After reducing the model by backward selection only Year, Date, Sex and the interaction between Date and Sex remained. The quadratic term and all other interactions were not statistically significant.

Other statistical procedures
To test for annual changes in longitude and latitude of resighting locations elsewhere in Europe, Kruskal-Wallis tests were applied (SPSS 16). Sampling effort was not corrected for, as over the years, numbers ringed in Fryslân decreased (1138 in 2004, 1256 in 2005, 969 in 2006, 730 in 2007 and 523 in 2008), the proportion of marked individuals in Fryslân remained constant around 3%, and the sample size of observations outside The Netherlands was fairly constant with 21 in 2005, 41 in 2006, 36 in 2007 and 47 in 2008.

Results

Population trends
In Fryslân, the number of migrants declined (Fig. 7.1), which significantly affected peak migration counts (16-30 April, r_s = -0.99, p< 0.0001). The migrant population involved 25,000 ruffs in 2001, but in 2010 only 5000 remained. Counts corrected for length of stay showed a similar decline in migrants, from 18,673 in 2006, to 18,273 in 2007 and 10,077 in 2008. In Pripyat, peak migration significantly increased from less than 5000 to 30,000 migrants (16–30 April, r_s = 0.71, p = 0.02).

In Fryslân, the phenology (expressed as the proportion of birds passing through in late April and early May) did not vary with maximum counts (Fig. 7.2). In contrast, in Pripyat with an increase in numbers of migrants, the phenology shifted forward, with an increasing proportion of migrants passing in April (Fig. 7.2).
Figure 7.1. Numbers of migrant ruffs passing through The Netherlands and Belarus between 2001 and 2010, in bimonthly periods. Given are numbers through six migration periods. Note that peak numbers generally appear in mid April in The Netherlands, and late April/early May in Belarus.

Figure 7.2. Spring migration phenology of ruffs in relation to peak number of migrants. For The Netherlands, 16–30 April signified peak migration; 1–15 May signified just after peak migration. In Belarus, peak migration is either between 16–30 April, or between 1–15 May, depending on maximum numbers passing.
Local staging performance
In radio-tagged birds tagged before 2 April, the minimal length of stay was 24.2 (± 8.7) in 2005 and 19.2 (± 11.3) days in 2007 (Fig. 7.3A). In colour-ringed birds, length of stay decreased significantly with year (posthoc Tukey test, F_{77, 2} = 96.2, p < 0.0001) (Fig. 7.3B), from 23.2 (± 2.8) days in 2006 to 18.5 (± 3.9) days in 2008.

Figure 7.3. Mean length of stay of migrant ruffs in The Netherlands. (A) Telemetry based estimates of minimal length of stay of adult males. (B) Colour-mark estimates of length of stay (mean ± 95% CI of bootstrap estimates) based on encounter histories of ornamented males ringed in year $i$ and resighted in year $i$. Horizontal lines indicate mean length of stays for each year. In right panel symbols for means mostly overlap with 95% CIs.

Figure 7.4. Refueling rates of migrant ruffs in The Netherlands (black lines) and in Belarus (grey lines). Mass gain rates are slopes of generalized least squares (GLS) regressions of body mass on date. The solid lines are Restricted Maximum Likelihood (REML) estimates of body mass increase; the dashed lines are REML estimates of body mass increase scaled to wintering conditions (wint_cond).
The rate of body mass accumulation showed a significant year by location interaction ($L_1, 11732 = 248, p < 0.001$): over the years the rate decreased in Fryslân, but remained stable in Belarus (Fig. 7.4). A significant and parallel effect of wintering conditions on refueling rate was detected ($L_1, 11732 = 6.72, p < 0.01$). At both locations the rates were relatively high in 2003 and 2005, which were the drier winters. This was true for both adult males ($n = 7367$), females ($n = 3338$) and 2cy males ($n = 1027$, see Supporting Information). Annual variation in arrival body mass did not vary significantly between locations ($L_1, 112 = 0.006, p = 0.94$), and was stable in females and 2 cy males, and slightly decreased in adult males in Belarus. In Fryslân, moult was halted at significantly earlier stages in later years (Fig. 7.5).

![Figure 7.5. Moult into breeding plumage of migrant ruffs in The Netherlands. Given is the mean growth stage of ruff feathers in ornamented adult males.](image)

Resighting of marked individuals

Of ruffs marked in Fryslân since 2004, 145 observation of individuals re-sighted elsewhere on northward migration in any subsequent spring were obtained (Fig. 7.6). The longitude of the resighting locations of these 145 observations varied significantly between years (Fig. 7.6; $X^2_3 = 12.2, p = 0.007$), with a trend towards easterly resightings from 2004 to 2008.

Discussion

There are few known examples of rapid shifts in direction and distribution of migration routes of birds, with the best known example being that of evolution of new wintering areas over a few generations in the blackcap *Sylvia atricapilla*, a European passerine (Berthold *et al.* 1992). The observed gradual change in longitude of resightings of individuals marked in The Netherlands during the first decade of 21st century
reflects increasing numbers of individuals using eastwards routes. As the Dutch migrants declined twice as fast as the European breeding numbers (see below), we suggest that many formerly Dutch migrants have made the switch to eastern migration routes. Hence the decline of Dutch migrants would be the result of changes in site use rather than a reduction in global population size. This is to our knowledge the first report of a rapid shift within the generation time of a migratory species.

**Trends in relation to the global population**

Migrant ruffs from The Netherlands winter predominantly in the Sahel (OAG Münster 1989; Zwarts *et al.* 2009). Since the 1950s, major shifts in the winter distribution of ruffs have occurred, especially with respect to the use of areas in Senegal, but the numbers wintering in the larger area are considered to have been stable over the last two decades (Zwarts *et al.* 2009). Alternatively, declining breeding numbers in Northwest Europe (Zöckler 2002; Thorup 2006) might explain the decline of Dutch migrants. However, the 6% annual rate of decline of the Dutch migrants exceeds the declines of 2.1-2.9% per year for ruffs breeding in the European Arctic (estimates for
1990-2007; Chapter 8), and the 3% for the total European grounds (estimates for 1994-2004, BirdLife International (2008)).

The Dutch migrants mainly consist of males (Jukema et al. 2001; Verkuil & de Goeij 2003), but ruff numbers are usually monitored by counting breeding females (as males do not nest, Hogan-Warburg (1966)). Hence, the greater decline in the passage than in the breeding numbers might be explained by sex-specific differences in population trends. This is unlikely, however, as local trends in refueling rates are similarly negative in males and females, with females even approaching a situation of zero mass gain rates (Fig. 7.4). Females would thus be expected to be negatively affected by staging conditions in Fryslân even more than males.

Additional anecdotal evidence supports the shift of many formerly Dutch migrants. In Pripyat, the recapture rate of ruffs colour-marked in Western Europe changed from 0 of 3,499 captured individuals between 2001-2007, to 5 out of 2,335 in 2008. The five recaptures in 2008 refer to three individuals marked in Fryslân (captured 5 April 2003, 6 April 2006, 24 April 2006) and two marked in Sweden (captured 31 August 2003, 17 May 2007).

Changes in habitat quality in The Netherlands

The contrast between the staging performances of the Dutch and Belarusian migrants suggests that the decline in Fryslân is a local phenomenon. The shortened length of stays, decline in refueling rate and the halting of moult at increasingly earlier stages indicate that conditions have deteriorated. Refueling and moulting are major determinants of a successful migration (Alerstam & Lindström 1990; Zwarts et al. 1990; Lindström 2003; Baker et al. 2004; Piersma & Lindström 2004). Unsuccessful ruffs might discontinue the use of a staging site that no longer offers good conditions.

There are, however, two alternative explanations for the decline in staging performance. Firstly, the quality of sites used before arrival, could have changed. However, no long-term change in arrival body mass was detected. Furthermore, we found parallel effects of wintering conditions in both staging populations. At both staging sites, refueling rates are generally higher after dry winters, but in later years this compensation was lower in Fryslân than in Pripyat (Fig. 7.4). Also, moult at the staging site starts from zero (Jukema & Piersma 2000), so the halting of moult at earlier stages in Fryslân will mainly be a local effect. Secondly, the composition of the population could have changed; birds with high refueling rates might have disappeared from the staging site for another reason than declining local habitat quality. Yet, preliminary analyses on local return rates of marked individuals suggest that ruffs with advanced facial wart development in the previous year were more likely to return (facial warts are a carotenoid-based, diet-dependent sexual trait). Also the timing of migration did not change in Fryslân. We therefore conclude that a quality change of the staging habitat and not a change of the migration population have influenced staging performance.

Staging performance can change due to a decline in (a) quantity of quality of food resources or a (b) decline in availability of food resource, e.g. when predation risks
increases staging time might decrease (Ydenberg et al. 2004). In Fryslân, raptor abundance in general, and abundance of the main predator, peregrine falcon *Falco peregrinus* did indeed increase in the 1990s and earlier (A: solid black line). In 2000s this habitat type became scarcer (B: solid black line). Recently, staging ruffs predominantly use manure-injected agricultural grassland. The occurrence of manure-injected fields decreases with date (B: black dashed line) as farmers apply manure early in the season thus allowing an early grass harvest. As a result ruffs have to leave the staging site earlier and the overall capacity of the staging area decreased.

In Fryslân, ruffs foraged predominantly in agricultural grasslands. These grasslands are managed intensively, most fields being highly fertilized monocultures of *Lolium perenne* with low water tables and early mowing dates. The sensitivity of ruffs to drainage of grasslands (Thorup 2004), resulted in the cessation of breeding of ruffs in The Netherlands (Bijlsma, Hustings & Camphuysen 2001), and temperate Europe (Hötker 1991; Zöckler 2002). Drainage also affected the Dutch migrants. They encountered low availability of the preferred medium herb-rich grasslands with a high water table; the alternative ‘habitat’ used by ruffs since the wet grasslands disappeared, are freshly manure-injected *Lolium perenne* monocultures (Verkuil & de Goeij 2003). The application of manure drives soil organisms to the surface, which enhances prey

Figure 7.7. Relationship between numbers of staging ruffs and habitat availability in The Netherlands. The preferred habitat of ruffs is wet agricultural grassland (Verkuil & de Goeij 2003) which was available in 1990s and earlier (A: solid black line). In 2000s this habitat type became scarcer (B: solid black line). Recently, staging ruffs predominantly use manure-injected agricultural grassland. The occurrence of manure-injected fields decreases with date (B: black dashed line) as farmers apply manure early in the season thus allowing an early grass harvest. As a result ruffs have to leave the staging site earlier and the overall capacity of the staging area decreased.
availability temporarily (for one day). In recent years, manure injection has started earlier to enable an early first cut of grass (Schekkerman & Beintema 2007), leaving staging ruffs after mid April with fewer manure-injected fields (Fig. 7.7). Moreover, after mid-April drained fields in most years become impenetrable for shorebirds feeding on subsurface soil organisms (B. Verheijen and N. Groen, pers. comm.). The fact that the Dutch passage population depends to a great extent on manure-injection practices (Fig. 7.7) suggests that the availability of more natural fields has dropped below sustainable levels. The ongoing decline of the Dutch migrants indicates that for ruffs the changes in agricultural practice and reduction in food availability has pushed the ecological bottleneck for refueling and ornament development below sustainable levels (Buehler & Piersma 2008).

**Mechanisms for flexible migration**

How flexibly animals can respond to environmental change will largely depend on their ability to change behaviour. Our results show that migratory animals can change spatial distributions, and hints at processes causing a change. The observed gradual increase in longitude can reflect (a) a gradual shift in longitude of individuals or (b) increased numbers of individuals shifting. A gradual shift would be the reflection of a site-sampling process. If the move is a one-time shift of individuals with no site-sampling involved, this would hint at a winter-driven process. The observation that wintering conditions affect the Belarusian and Dutch migrants in the same way suggests that both winter in the Sahel or in adjacent regions where rainfall and evaporation conditions correlate with the conditions in the Sahel. Shared wintering location might enhance exchange of information. We have no insight in how information exchange would occur and why it should have changed. It would require advanced inference by individual birds or possibly flock-based migration decisions during departure from wintering grounds (see Bijleveld et al. (2010)). Either way, there is definitely a scope for studies on mechanisms for flexible migration.

**Acknowledgements**

We thank the Frisian wilsternetters for catching ruffs, and colleagues and students who worked with us in Fryslân and at the "TUROV" Ringing station. We are grateful to all volunteers for counts and resights. Catching, ringing and tagging activities were covered by required licences under the Dutch and Belarusian laws. Kathryn Hine processed the radio-telemetry data. Nils Warnock, Tomas Gunnarsson, Popko Wiersma, Jutta Leyrer, Arne Hegemann and Maryann Burbidge provided useful comments on earlier drafts. The Dutch part of this study was financed by a start-up grant to TP from the University of Groningen, by grants of the GUF/Gratama Foundation (project 04.05) to YIV and the Schure-Beijerinck Popping Foundation (SBP/JK2006-39 and SBP/JK2007-34) to YIV and JCEWH.