Losing a staging area: Eastward redistribution of Afro-Eurasian ruffs is associated with deteriorating fuelling conditions along the western flyway

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ARTICLE INFO

ABSTRACT

The fuelling performance of long-distance migrants at staging areas indicates local conditions and determines the viability of migration routes. Here we present a first case study where long-term fuelling performance was documented along two migration routes with differential population trends. Ruffs (*Philomachus pugnax*) are shorebirds of inland freshwater wetlands that migrate from the sub-Saharan wintering grounds, via Europe, to the northern Eurasian breeding grounds. Assessments from 2001 to 2008 of fuelling during northward migration at the major western and eastern staging site revealed that daily mass gain rates steeply declined across years in the grasslands for dairy production in Friesland, The Netherlands, and remained constant in the Pripyat floodplains in Belarus, 1500 km further east. Migrants in Friesland decreased from 2001 to 2010 by 66%, amounting to a loss of 21,000 individuals when counts were adjusted for length of stay as determined by resightings. In the same period numbers in Pripyat increased by 12,000. Ruffs individually ringed in Friesland were resighted in subsequent springs at increasingly eastern sites including Pripyat. Our results corroborate published evidence for an eastward redistribution of Arctic breeding ruffs and suggest that the decreasing fuelling rates in the westernmost staging area contribute to this redistribution. The shift implies that responses occur within a single generation. The hypothesis that the choice of route during northward migration may be driven by food availability can now be tested by creating greater areas of wet grasslands in Friesland. When local staging conditions improve we predict that ruffs will make the reverse shift.

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1. Introduction

Due to global change, animal migrations are rapidly becoming endangered phenomena (Wilcove and Wikelski, 2008). For example, fish and large herbivores may find man-made obstructions and habitat destruction blocking their migration routes (Berger, 2004; Rolls, 2011). Birds that make intercontinental migrations encounter similar problems (Sanderson et al., 2006). Especially the ecologically specialized shorebirds are vulnerable (Piersma and Baker, 2000). Ecological deterioration of staging sites, where fuel stores are rebuilt for subsequent flights (Lindström, 2003), has recently led to flyway-wide population declines in four of the six known subspecies of the red knot *Calidris canutus* (*rufa*, Baker et al., 2004; *islandica*, van Gils et al., 2006; *piersmai* and *rogersi*, Rogers et al., 2010). Red knots may not be able to shift to alternative fuelling areas or migration corridors because they depend on limited intertidal habitats. Migratory shorebirds whose migration corridors are not confined to coastal or otherwise restricted habitats could have such opportunities (Piersma, 2007).

In this light it is pertinent that ruffs *Philomachus pugnax*, using widespread freshwater wetlands including agricultural grasslands, recently showed a large-scale eastward redistribution from the European into the Asian part of their Arctic breeding range (Rakhimberdiev et al., 2011). This was hypothesized to be a consequence of avoidance of staging areas in Western Europe, due to

deteriorating local ecological conditions. Here we assess this suggestion by comparing fuelling performance at two areas used by ruffs wintering in the savannas of sub-Saharan Africa, the Sahel, during their northward migration (Zwarts et al., 2009).

The total population of ruffs counts >2 million individuals, but this estimate is considered imprecise; there is also little information on trends in the wintering and breeding areas (Girard et al., 2009; but see Rakhimberdiev et al., 2011). The wintering population of ca. 400,000 ruffs in the western Sahel has been stable in this century (Zwarts et al., 2009). In spring these ruffs use two main migration corridors, one over Western Europe mainly leading to breeding grounds in temperate Europe and the European Arctic, and one over Eastern Europe leading to Western and Central Siberia (Fig. 1). Currently, three major staging areas during northward migration, each with over 10,000 ruffs, are known: (i) the agricultural grasslands, intensively managed for dairy production, in the province of Friesland, The Netherlands (Jukema et al., 1995), (ii) the extensively managed floodplain meadows of the Pripyat, Belarus (Mongin and Pinchuk, 1999), and further east (iii) the shallow water lagoons (limans) of the Sivash, Ukraine (Chernichko et al., 1991). During staging, birds increase in mass and store fat (Jukema et al., 1995), and most of the males moult intensely as they develop ruffs, tufts and facial masks (Jukema and Piersma, 2000). The combined activities of fuelling and ornament development increase energetic requirements at their staging areas during northward migration (Buehler and Piersma, 2008).

The passage population of ruffs in Friesland has been in decline, especially in the last decades. Peak numbers in spring decreased from 50,000 to 60,000 during the 1990s to 8000 in 2008 (Wymenga, 2005; Wymenga and Sikkema, 2011). To test whether the ongoing decrease of the Dutch staging area is related to local fuelling performance we assessed population size corrected for individual length of stay (LOS), and we measured rates of seasonal body mass increase in the springs of 2001–2010. A parallel study in the Pripyat, 1500 km further east (Karlionova et al., 2007; Meissner et al., 2011), permitted a comparison between two flyways.

2. Methods

2.1. Field techniques

The study area in Friesland (400 km², centred on 52°58′ N 05°24′ E) is dominated by dairy farms and accommodates on average 77% of the ruffs migrating through Friesland in spring (Wymenga, unpubl.). From March until May ruffs feed here on invertebrates found in grasslands. In 2001–2010, the roost sites along shallow lake shores, covering the core staging area, were counted semi-monthly by volunteers (Hooijmeijer et al., 2010). Counts were made within ±3 days of the 1st and 15th of March, April, and May. Additionally, in this period we captured ruffs at a maximum of 10 sites simultaneously with wind-driven clap nets. A flock of artificial decoys and 1–2 live decoys captured at the start of the session and released afterwards, were used to lure flying birds to the net. Captured ruffs were given a numbered metal ring and weighed. Straightened wing length was measured. Birds with wings ⩽170 mm were classified as females, and those with wings >180 mm as males that usually develop ornaments (see Karlionova
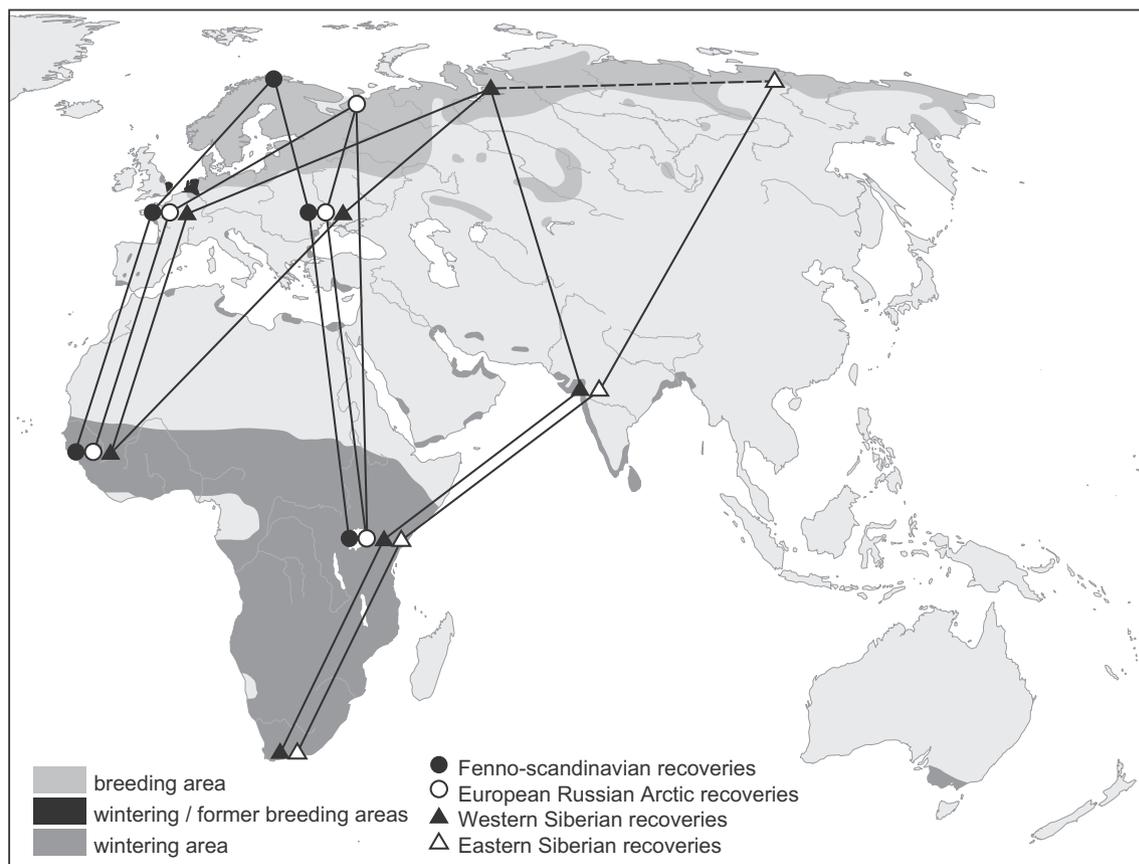
Fig. 1. Schematic overview of the flyways of ruffs *Philomachus pugnax*. The symbols signify four regions of the global breeding range. The lines summarise 364 long-distance recoveries of ruffs ringed in wintering or breeding sites, and >1000 recoveries of ruffs ringed in Western and Eastern Europe and recovered elsewhere. Solid dark grey: wintering areas. Solid light grey: the temperate and arctic breeding areas in Europe and Russia. Note that the Arctic harbours c. 95% of the global population of the ruff; numbers in the temperate breeding areas are minor and strongly declining. In black: former temperate breeding areas (modified after Zwarts et al., 2009).

et al., 2008). Non-ornamented small males with wings between 170 and 180 mm (so-called faeders, Jukema and Piersma, 2006), occurred in low frequencies (around 1%; Verkuil et al., 2008) and were not considered. Birds were aged by leg and plumage characteristics (Meissner and Scebba, 2005; Meissner and Ziêcik, 2005).

From 2004 onwards migrants were colour-marked in Friesland. Each captured ruff was given a unique combination of four colour bands and a coloured flag. The study area was searched daily for colour-ringed ruffs between 25 March and 15 May 2004–2008. We fitted 48 adult males with radio-transmitters in 2005 and 47 more in 2007 (see Verkuil et al., 2010). Automatic receiving stations (ARTSs) with a maximum range of 5 km, erected at the nine main roosts spanning the total study area, continuously sampled individuals at 20 min intervals collecting a maximum of four signals each 20 min from 25 March to June 1. An individual was considered present if three out of four signals were positive; a signal was considered positive when the signal strength was 1.5 stronger than the noise level (Green et al., 2002).

The Pripyat river flood plains (Belarus, Turov, Gomel Region; centred on 52°04′ N 27°44′ E) support ruffs annually between March and May (Mongin and Pinchuk, 1999). From 2001 onward, we caught ruffs daily on a set of small islets in the floodplain, totalling about 2 km², mainly with walk-in traps and occasionally with mist-nets (Meissner et al., 2011). Each captured ruff was ringed with a numbered metal band, weighed, aged, and sexed as described above. From 1 March to 31 May, the roost site near Turov, which represents part of the Pripyat floodplains used by ruffs, was counted on 18–75 evenings (median 48 evenings), except in 2001, when only 7 counts were made. As the LOS > 10 days (Karlionova and Pinchuk, unpubl.), in 2002–2010 the peak of migration was always detected.

2.2. Overview of data analyses

The maximum count of each half month was used to enable comparisons of the counts in Friesland and Pripyat. Annual changes in the number of migrants were assessed by calculating the correlation coefficient (r_s) between year and the maximum count during peak migration in the second half of April.

Census size of the Friesian population was adjusted for LOS, obtained from capture–recapture analyses on colour-marked individuals (see below). Only LOS of (ornamented) males was estimated. Annual variation in LOS was determined to gauge possible changes in spring phenology. Sample sizes obtained for females were insufficient, as females are relatively scarce in Friesland because they traditionally use easterly routes (Wymenga, 1999), possibly related to differential habitat requirements (Verkuil and de Goeij, 2003). Radio-tagged males were used to obtain an independent estimate of LOS.

Fuelling rates were estimated by regressing body mass on date. Samples sizes of females were sufficiently high to be included. To account for carry-over effects from wintering sites (see Harrison et al., 2010), a winter condition effect (WCE) was incorporated as a covariate. To quantify WCE, the extent of floods (km²) in the Sahel during the preceding winter was used. Flooding of the river systems largely determines the size and quality of feeding areas of ruffs: a large flood extent is critical to their winter survival (Zwarts et al., 2009). The extent of floods in the Senegal and Inner Niger deltas was reconstructed by Zwarts et al. (2009) using annual river discharge data at Bakel (14°54′ N 12°27′ W) and Akka (14°51′ N 7°17′ E), respectively; impacts of dams were accounted for and the estimated surface areas were verified with satellite images. The total flood area was 13,625 km² in winter 2000–2001, 13,907 km² in 2001–2002, 10,874 km² in 2002–2003, 15,433 km² in 2003–2004, 10,874 km² in 2004–2005, 12,390 km²

in 2005–2006, 13,458 km² in 2006–2007 and 14,602 km² in 2007–2008.

2.3. Population size and length of stay

Following Frederiksen et al. (2001), we estimated the size of the population in Friesland using:

$$N_{new, current} = N_{total, current} - N_{total, previous} \times \varphi_{previous \rightarrow current},$$

where $N_{new,current}$ is the current number of new birds, $N_{total,current}$ is the total count in the current period, $N_{total,previous}$ is the total count during the previous period, and $\varphi_{previous \rightarrow current}$ is the local survival or staying probability from the previous to the current period. Estimates for φ were obtained from mark-recapture survival analysis (see below). As census data were collected bimonthly, a cumulative 14-day staying probability was calculated by multiplication of 2-day staying probability estimates (see Dinsmore et al., 2002). Because there was no indication of emigration in March and the staying probabilities late in March were very close to 1, the staying probability of the first ruffs arriving in the interval 1–24 March was set to 1. Estimated population size was the sum of $N_{new,current}$ for all 14-day periods. The variance of the annual sum was obtained by bootstrapping with a million iterations; survival probabilities for each 2-day staying period were taken at random from the normal distributions with means and SE obtained from the survival analysis. Birds counted between 1 and 15 March were considered new arrivals; as numbers in March were low this assumption does not markedly affect the grand total.

To estimate LOS with mark-recapture analysis, for the colour-marked males encounter histories with 2-day intervals were generated, beginning on 25 March in the year after marking (so all encounter occasions were sightings and not catches). We did not use newly ringed birds as they have slightly longer staging times (Verkuil et al., 2010). This resulted in 113, 461, 451 and 437 encounter histories respectively in 2005, 2006, 2007 and 2008. Only 2-day time intervals with >9 resightings were used (Morris et al., 2006). This requirement was not met for most intervals in 2005, so this year was excluded. In the other years only data after 4 May were discarded. Over the remaining 20 intervals the 2-day resighting probabilities varied between 0.11 and 0.17 (Verkuil et al., 2010).

Mark-recapture logit selection procedures were conducted according to Pradel (1996). The global Goodness-of-fit test to the fully time-dependent Cormack–Jolly–Seber (CJS) model (see White and Burnham, 1999), executed with U-CARE version 2.3, M7.2 (Choquet et al., 2009), was not significant ($\chi^2_{874} = 870.41$, $P = 0.528$, $\hat{c} = 1$). This indicated that the CJS model was acceptable. The CJS model assuming annual variation in staying probability ($\varphi_{t+y} p_{t \cdot y}$) was significantly different from $\varphi_t p_{t \cdot y}$ ($\Delta AIC = 4.63$, see Table 3 in Verkuil et al. (2010)). In the SODA programme (Schaub et al., 2001) LOS can only be estimated for each year separately, so model selection was repeated for each year. In all years, the models assuming that φ and p are date-dependent ($\varphi_t p_t$) were the most parsimonious ($\Delta AIC = 9.6$, 7.9 and 5.3 in 2006, 2007 and 2008, respectively).

The date-dependent models were used to generate estimates of LOS by bootstrapping in SODA; LOS is the sum of duration of stay after encounter and duration of stay before encounter. For each of the 20 time intervals in each year, 300 estimates for LOS were obtained by bootstrapping because they converged at 200 iterations. The normally distributed estimates were analysed with a general linear model to assess annual variation in LOS, with year as categorical factor and Date as co-variable (SPSS 16).

For radio-tagged birds, capture-recapture modelling did not apply, as the initial seasonal encounter was the capture occasion,

which violates the assumption of equal encounter probabilities for each time interval. The minimal LOS (days between tagging and last recording; Warnock et al., 2004) was calculated using only birds from the first two tagging cohorts (24–26 March and 1–2 April; $n = 20$ in 2005, $n = 22$ in 2007) to avoid underestimates.

2.4. Fuelling rates

To estimate fuelling rates, we applied the modelling approach of Zuur et al. (2009) in 'R' (R Development Core Team, 2008). We estimated population average fuelling rates (insufficient recaptures were made to estimate individual mass gains). When comparing mean mass gains, variations in arrival time will lead to apparent (but not real) variation in fuelling rates. To account for local and yearly variation in timing of migration, date was centred as: Date − (firstday(for each place and year) − lastday(for each place and year))/2 and converted to the positive value (centred date − (overall minimum of centred date) + 1). The median catching date was not used as the proportion of birds caught at a specific date did not correspond with the total number of birds present at that date; thus, the most reliable measures were from the first and last days of catching. Year was treated as a continuous variable and therefore transformed to Year − min(Year) + 1. This transformation makes the intercepts more useful as it will differentiate between 0 and Y_i when $i = 0$. The variable WCE was scaled by the 'scale' R function; scaling divides the (centred) columns of x by their standard deviations. The first general linear model (LM) included Bodymass as the response variable, with explanatory variables Date, Year, Place, Group (adult males, second calendar year males, females) and WCE. This LM 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 generalised least squares (GLSs) method was applied. The initial model included BodyMass as

response variable and explanatory variables Date, Year, Place, Group and WCE and all their interactions, except between Year and WCE. 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 and reduced by standard backward selection of interactions (Zuur et al., 2009). For the final model with remaining interactions see Appendix S1.

We modelled arrival body mass separately for Friesland and Pripyat, and defined arrival body mass as the body mass of the first 15% of birds caught in each place in each year. This cut-off of 15% yielded only enough data for adult males, the vast majority of early arrivals. No heterogeneity of variance was found and hence a general linear model was applied to model the relationship of body mass with year. Between – year differences were not tested for, as data were insufficient to treat year as a categorical variable.

3. Results

3.1. Population trends

From spring 2001 to spring 2010, the maximum number of migrant ruffs counted at roosts in the study area in Friesland declined on average 8% per year (Fig. 2); in Friesland as a whole this figure averaged 15% annually over 1998–2008 (based on four censuses, Wymenga and Sikkema, 2011). The counts during the peak of the migration (16–30 April) in the study area decreased significantly ($r_s = -0.99$, $P < 0.0001$). In 2010 fewer than 4000 ruffs remained of the migrant population that consisted of 19,200 individuals 10 years earlier. The estimated population size in Friesland showed
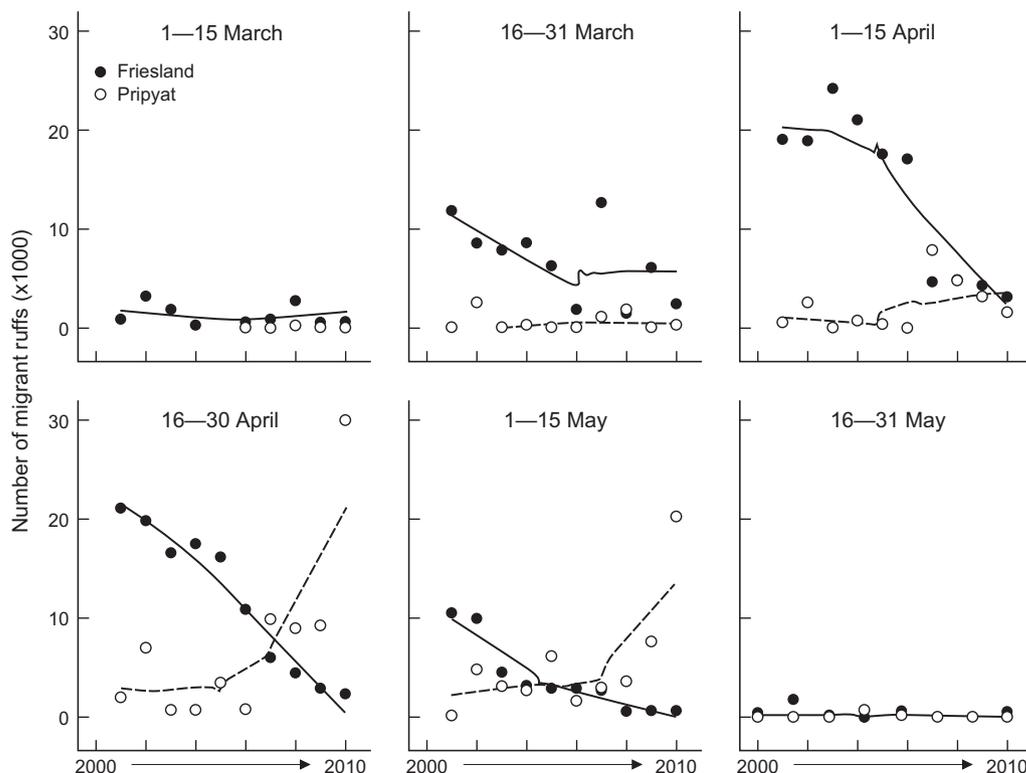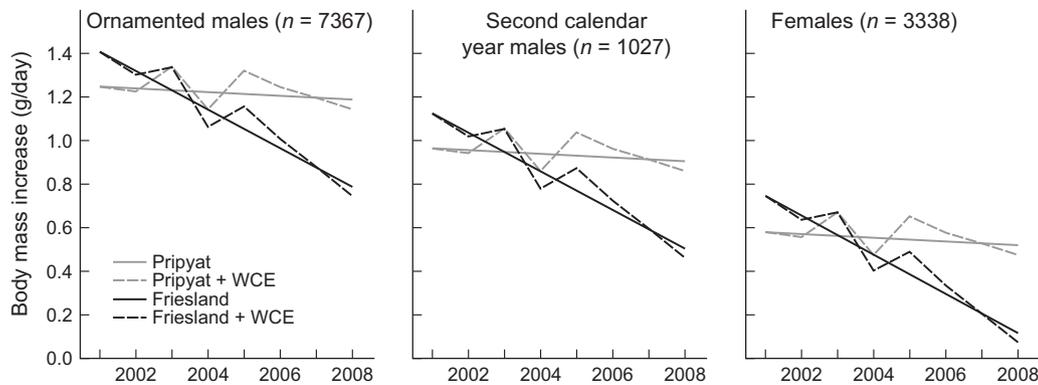

Fig. 2. Numbers of migrant ruffs passing through the study area in Friesland, The Netherlands (black) and Pripyat, Belarus (white) between 2001 and 2010. Given are numbers through six migration periods of 2 weeks. Lines are running averages.

Fig. 3. Fuelling rates of migrant ruffs in Friesland, The Netherlands (black lines) and in Pripyat, Belarus (grey lines). Mass gain rates are slopes of generalised least squares (GLSs) 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 winter condition effect (WCE).

a similar decline: from a median of 30,849 (95% CI 15,691–31,181) in 2006, to 13,716 (10,480–13,716) in 2007 and 9731 (4893–9731) in 2008. In the Pripyat study area, numbers during peak migration increased from on average 2508 migrants in 2001–2006 to on average 14,546 migrants in 2007–2010 (16–30 April, $r_s = 0.71$, $P = 0.02$). The migration cohort in May was stable (Fig. 2), but between 2007 and 2010, in Pripyat a much larger April cohort appeared than in earlier years.

3.2. Length of stay

For ornamented males colour-ringed in Friesland, LOS was significantly different between years ($F_{2,57} = 96.2$, $P < 0.0001$), decreasing from 23.4 ± 2.8 days in 2006 ($n_{ind} = 461$), to 21.1 ± 3.0 days in 2007 ($n_{ind} = 451$) and 18.5 ± 3.9 days in 2008 ($n_{ind} = 437$). For males radio-tagged before 2 April, a similar trend was observed: the minimal LOS was 24.2 ± 8.7 days in 2005 ($n_{ind} = 20$) versus 19 ± 11.3 days in 2007 ($n_{ind} = 22$).

3.3. Local staging performance

Fuelling rates showed a significant year by location interaction ($L_{1,11732} = 248$, $P < 0.001$). In Friesland, over the period 2001–2008, fuelling rates of adult males decreased from 1.4 to 0.8 g day^{-1}, in second calendar year males from 1.2 to 0.5 g day^{-1} and in females from 0.7 to 0.2 g day^{-1} (Fig. 3). Between 2001 and 2010 fuelling rates remained stable in Pripyat at ca. 1.2 g day^{-1} in adult males, ca. 1.0 g day^{-1} in second calendar year males and ca. 0.6 g day^{-1} in females (Fig. 3).

A significant and parallel effect of winter conditions on fuelling rate was detected in both staging areas ($L_{1,11732} = 6.72$, $P < 0.01$). Fuelling rates were relatively high in 2003 and 2005, which followed drier winters in the Sahel. In Friesland arrival body mass in adult males was stable across years at 181 ± 22SD g ($F_{1,920} = 1.66$, $P = 0.20$). In Pripyat arrival body mass of adult males decreased from 208 ± 20SD g to 182 ± 32SD g between 2001 and 2008 ($F_{1,802} = 96.63$, $P < 0.0001$).

4. Discussion

From 2001 to 2010, the fuelling rates of the declining ruff population in Friesland decreased by 43% in males and 71% in females, and the LOS in ornamented males decreased by 21%. Over the same period in the increasing population in Pripyat fuelling appeared stable. The regression of mean body mass on date to estimate fuelling rates is a method that must be applied with caution because the arrival of different cohorts would result in underestimates

(Zwarts et al., 1990; Gillings et al., 2009). In Friesland, LOS decreased over the years, but this was due to earlier emigration (Fig. 2) and earlier analyses show that arrival time did not change over time (Verkuil et al., 2010). Pripyat may have hosted two separate cohorts in later years and this could have obscured a possible increase in fuelling rates.

To explain the measured decrease in fuelling rates in Friesland, the following, non-exclusive explanations can be suggested: (i) habitat change elsewhere in the flyway, (ii) adjustments to a different phenology, and (iii) change of local habitats. The observed population decline might signify (i) a decline of the breeding population and/or (ii) shifts to alternative staging sites.

4.1. Changes along the flyway

The decrease in fuelling performance in Friesland could be due to changes at wintering grounds or at prior migratory sites. As ruffs fly directly from Africa to Central and Western Europe (OAG Münster, 1989), an effect of prior staging is unlikely. Regarding the wintering grounds, ringing has shown that migrants from Friesland and Pripyat winter in the same areas in the Sahel (Zwarts et al., 2009). Indeed, the parallel carry-over effect of the extent of winter floods on fuelling suggested that the populations come from shared wintering grounds. The higher fuelling rates after dry winters might suggest that ruffs were compensating after arriving with small nutrient stores. However, the data on arrival body mass did not allow analyses at the level of these specific winters. Linear models showed that over time arrival body mass was constant in Friesland, suggesting stable winter conditions, and decreased in Pripyat to the same level as in Friesland. This decrease in Pripyat could well be related to the early arrival of the new cohort. Habitat deterioration in the Sahel and others threats like hunting (Zwarts et al., 2009) could theoretically have reduced arrival body mass in Pripyat and numbers in Friesland, but this still would not explain the increase in numbers in Belarus and the decrease in staging performance in Friesland.

4.2. Changes in phenology

Staging performance may have declined because the phenology might have changed, resulting in migration schedules that allow for lower fuelling rates (i.e. extended LOS). In Friesland no extended LOS was detected. On the contrary, LOS decreased. However, this does not eliminate the possibility that birds with high refuelling rates have disappeared disproportionally. Whether high-quality ruffs, as indicated by ornament development, still return to Friesland has to be confirmed by future analyses on

differential survival in our colour-marked population (Sandercock, 2003).

4.3. Local changes in Friesland

Alternatively, the observed changes in staging performance might be due to local habitat changes in Friesland. In Friesland ruffs predominantly forage in agricultural grasslands. The sensitivity of breeding ruffs to drainage of grasslands (Thorup, 2004) and related intensification of land use resulted in the virtual cessation of breeding in The Netherlands (Bijlsma et al., 2001) and the rest of temperate Europe (Hötker, 1991; Hagemeijer and Blair, 2009). In the study area ground water tables have been lowered by more than half a metre since 1950 (Schroeder et al., 2011), while drain pipes are used more frequently to drain the top soil of grasslands. This type of water management leads to a lower abundance and availability of soil invertebrates for soil-probing predators (e.g. Klein et al., 2011). Ruffs currently encounter low availability of their preferred non-tilled herb-rich grasslands; 68% of the foraging fields used by ruffs in the study area are frequently-tilled, manure-injected *Lolium perenne* monocultures which lie high above the water table (Verkuil and de Goeij, 2003).

The relevant environmental measurements to put the observed decline in context are currently incomplete. We outline three changes with known affects on grassland birds (see Donald et al., 2001) that require further examination because they may limit food intake rates. (i) Since the implementation of the European Union Nitrates Directive of 1991, injection is the common method for the application of slurry (semi-liquid manure) on farmland. Slurry injection creates an initial food peak for a few days but subsequently depletes soil invertebrates for up to 4 weeks (Oosterveld, 2006). Recently new techniques are applied, by which the slurry is transported to the injector by pipes instead of attaching a storage tank to the injector. This allows for earlier injections in spring and produces an early first cut of grass. The advanced injections may mean that ruffs can no longer capitalise on the resulting food peak. (ii) In Friesland there is a trend towards lack of rainfall in spring (April 1999–2010; $R^2 = -0.66$, $P = 0.02$, station Leeuwarden, KNMI (2011)). If this trend persists, it would reduce the penetrability of soils, and negatively effect prey availability in other ways also. (iii) Between 1997 and 2009 the proportion of dairy cows kept permanently inside stables increased from 8% to 24% nationwide (CBS, 2010). Ungrazed parcels with dense grass swards are unattractive to ruffs, especially from mid-April onwards, whereas grazed parcels offer ample feeding opportunities (e.g. open vegetation structure, micro relief through trampling, cow cakes).

On the scale of the study area, the combined impact of the changed farming practices (drainage, more frequent tilling, advanced slurry injection, less grazing) may have limited the abundance and availability of soil invertebrates, exacerbated by dry springs. The potential impact of these changes on the food availability for grassland birds should be studied in experimental and socio-ecological contexts (Cooke et al., 2009).

Habitats in Friesland can also have deteriorated due an increase in predation risk (Ydenberg et al., 2004). In the late 1980s and early 1990s abundance of peregrine falcons *Falco peregrinus* correlated negatively with pre-winter energy storage in golden plovers *Pluvialis apricaria*, who share agricultural grasslands with ruffs (Piersma et al., 2003). Yet, raptor densities stabilized in the 1990s and 2000s (Bijlsma et al., 2007). Stable predator densities do not exclude an increase in predation, e.g. due to changes in landscape features that would allow for more surprise attacks (van den Hout et al., 2008). Ruffs behaviourally adjust by keeping away from landscape features that obstruct their view (Verkuil and de Goeij, 2003). Indeed, in the past decades the spring distribution of ruffs in Friesland changed to more open areas, which might be explained as predator avoidance (Wymenga and Jalving 2005).

4.4. Decline of the breeding population

Ruffs migrating through Friesland connect to both Fennoscandinavian and Russian breeding grounds (Zwarts et al., 2009) and hence the decline could be a secondary effect of the declines in breeding numbers in Northwest Europe (Thorup, 2006) and in the European Arctic (Zöckler, 2002). Consistent with the crash of the western breeding populations, at Ottenby, Sweden, where ruffs stage for a few days during southward migration, numbers have also declined steeply since the 1990s (Lindström et al., 2009). Rakhimberdiev et al. (2011) showed that in the last decade breeding ruffs have redistributed eastward into Asia. It is unknown, however, how much of the decline in western breeding birds is due to increased mortality or to the redistribution of breeding birds.

4.5. Shifts to alternative sites

If breeding birds have moved away from western breeding sites, the decline in Friesland could be due to birds shifting their flyway. Alternatively, the decrease in habitat quality of Friesland might have contributed to redistribution of breeding birds. Ruffs that shift to an eastern flyway during spring migration would end up breeding in other, more easterly, areas (Rakhimberdiev et al., 2011).

The increase of the early cohort of about 10,000 ruffs since 2007 in Pripyat could reflect a redistribution if ruffs from the Sahel with a Western European migration schedule would now take the eastern route and thus show up in Pripyat in April. Alternatively, it could reflect a shift in timing of migration, combined with fast population growth due to improved density-dependent survival at the wintering grounds now the Western European population is smaller. Since 2008, five ruffs ringed in Western Europe have been recaptured in Pripyat; in the earlier years no such recoveries were made. Three of these individuals were ringed in Friesland (captured 5 April 2003, 6 April 2006 and 24 April 2006) and two were ringed in Sweden (captured 31 August 2003 and 17 May 2007). This is a small sample, but resighting is improbable (see below).

Unfortunately, we cannot use the count data to assess whether population changes in the two areas are correlated, as increases in Pripyat only have occurred in the 3 years while in Friesland the decline has occurred over a longer period. To explore if Dutch migrants have moved, encounters of colour-marked individuals elsewhere on migration in any subsequent spring were collected. As of August 2010, 152 spring resightings were obtained, of which 14 were females. This small number, relative to the 5140 ruffs marked in Friesland in the years before 2010, is partly an effect of a low resighting probability outside Friesland, due to limited field time of observers, accessibility of habitats and, most importantly, population size. If marked ruffs use sites outside Friesland, they enter the population of *c.* 500,000 individuals that pass through the European sites (Zwarts et al., 2009). This means that the resighting probability in the rest of Europe is many times lower than in Friesland, where on average 1 in 36 ruffs is colour-marked (Verkuil, Hooijmeijer and Piersma, unpubl.). Hence, the chance that eastward movements of marked ruffs are discovered is rather small. Nevertheless, the sparse data indicate that between 2005 and 2010, the number of resightings did not change significantly in Fennoscandinavia while in Western Europe there was a trend towards fewer resightings, and in Central/Eastern Europe resightings increased significantly (Fig. 4, Appendix S2).
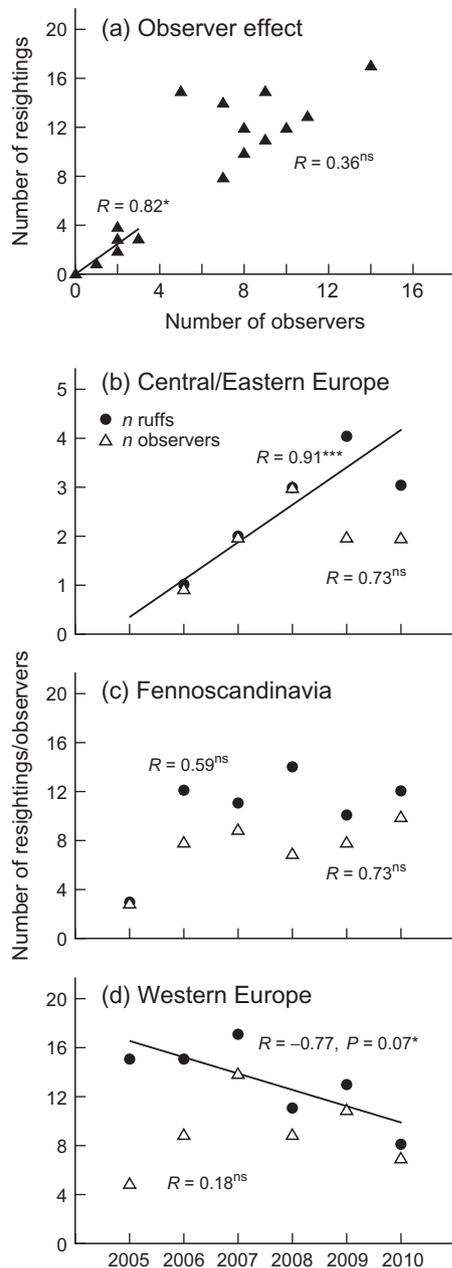
Fig. 4. Spring migration resightings between 2005 and 2010 of colour-ringed ruffs relocated outside The Netherlands ($n = 152$). (a) Relationship between the annual number of observers in a geographical region and annual number of observations. A significant observer effect was detected <4 observers. (b–d) Per geographical region, annual variation in total number of resightings (black) and number of observers (white). The number of observers did not significantly change over the years. Lines indicate significant trends. R indicates Pearson correlation coefficients; *$P < 0.05$; ***$P < 0.001$; ns, not significant.

4.6. Range shifts

Most breeding range shifts reported are northward expansions (e.g. Berthold et al., 1992; Thomas and Lennon, 1999; Parmesan and Yohe, 2003; Perry et al., 2005), elevation shifts (Moritz et al., 2008) or range reductions (Jetz et al., 2007), consistent with anthropogenic (climate) change (see Warren et al., 2001). There are known examples of rapid shifts in the direction and distribution of migration routes, although exclusively in long-lived bird species with extended parental care (Newton, 2007; Bauer et al., 2008; Dias et al., 2011). In his review of adaptive change of

migration routes, Sutherland (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 programme would steer the first southward migration and hence subsequent migrations; Böhning-Gaese et al., 1998). During first southward migration young ruffs travel independently of their parents (van Rhijn, 1991) and ruffs are therefore expected to use inherited navigation programs, but the rapid changes observed in Friesland and Pripyat seem to refute Sutherland's hypothesis. In ruffs flyway changes seem to have taken place within a single generation and therefore their innate program may not genetically constrain them to fixed migration routes (see Pulido, 2007).

5. Conclusion: a conservation experiment

The global redistribution of breeding ruffs and a possible shift to more eastern flyways (Rakhimberdiev et al., 2011) coincides with compromised staging performance and population decline in Friesland. The most likely cause for abandoning Friesland seems to be the current management of agricultural grasslands. We propose that the conditions for migrant ruffs can be improved relatively easily by elevating water tables, which indirectly steers land use, enabling the abundant earthworms Lumbricidae to remain abundant and available. The rapid pace of population changes detected in this study suggests that when conditions would improve ruff could quickly return to this staging site, assuming that ruffs are continuously sampling migration routes.

The individual ruffs that changed flyway may have been sampling sites independently; alternatively their dispersal could have been prompted by a flock-based decision after information transfer during wintering (Bijleveld et al., 2010). Possible individual triggers for flyway change could be examined by comparing dispersing and non-dispersing individual ruffs (see Clobert et al., 2009). The many reports of vagrant ruffs outside their range (in North and South America; M.K. Peck, pers. comm.) could be an indication that this species is particularly capable of colonisation (see Böhning-Gaese et al., 1998). The ability for flyway dispersal is expected to vary strongly between species (see Cote et al., 2010) and this behavioural variation needs to be addressed, particularly in shorebirds which globally are experiencing large scale habitat loss or deterioration (Boere et al., 2006), and especially along the East-Asian Australasian Flyway (Amano et al., 2010). The ability of rapid, major shifts would have important implications for our understanding of the potential responses of migratory species to environmental change.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2012.01.059.

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