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Authors: Vervoort, Raf, Schmaltz, Lucie E., Hooijmeijer, Jos C.E.W., Verkuil, Yvonne I., Kempenaers, Bart, et al.

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Within- and between-year variation in the presence of individually marked Ruff *Calidris pugnax* at a stopover site during northward migration

Raf Vervoort[1,2,*], Lucie E. Schmaltz[1], Jos C.E.W. Hooijmeijer[1], Yvonne I. Verkuil[1], Bart Kempenaers[2] & Theunis Piersma[1,3]

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Ruffs *Calidris pugnax* migrate from wintering areas in West-Africa and Europe to breeding grounds in northern Eurasia, using stopover sites along the way. At one such stopover site in southwest Friesland (53°N, The Netherlands), we studied variation in the timing of individual stopover based on 6474 Ruffs colour-ringed in 2004–2012. 43% of males and 22% of females were recorded in the study area in March–May the years following marking. Minimal stopover duration of returning individuals showed substantial within-year heterogeneity. We distinguished two classes: (1) 'transient' individuals were observed only on a single day in the study area within a season (51% of observed males and 79% of females), and (2) 'staging' individuals were observed on multiple days. We observed two seasonal peaks in the presence of transient Ruffs, typically coinciding with the peak of arrival and departure of staging birds. Males known to winter in Europe were more likely to be observed in the study area and arrived earlier than males of unknown winter origin (3.1 days and 3.7 days earlier for transient and staging males, respectively), but departure was unrelated to winter origin. Staging and transient females arrived later than males. Between-year repeatability of individual behaviour was low, and individuals did not significantly advance their arrival date over the course of years, in contrast with a pattern of shifting arrival dates at the population level. The observation that a large proportion of Ruffs visit southwest Friesland for only a short stop suggests that many individuals rely on other sites for moulting and refuelling during spring migration. Resightings of marked individuals elsewhere in western Europe indicated that these sites are largely located between 51° and 54°N. Thus, during spring migration, Ruffs marked in southwest Friesland displayed high between- and within-individual variation in minimal stopover duration.

Key words: shorebirds, migration, sex-related differences, farmland, agriculture, seasonal timing, staging, turnover, transience, *Philomachus pugnax*

[1]Rudi Drent Chair in Global Flyway Ecology, Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands;
[2]Department Behavioural Ecology & Evolutionary Genetics, Max Planck Institute for Ornithology, Eberhard-Gwinner-Strasse, 82319 Seewiesen, Germany;
[3]NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands;
*corresponding author (ribvervoort@hotmail.com)

During the northern summer, Ruffs *Calidris pugnax* breed in wet tundra across the Eurasian Low Arctic and in freshwater marshes and wet grasslands in the temperate zone (Cramp & Simmons 1983, Scheufler & Stiefel 1985). By 1990, wet grassland populations had severely declined in Western Europe (Scheufler &

Stiefel 1985, Zöckler 2002, Thorup 2006). Drainage of moors and wetlands and the changing use of previously extensively farmed meadows – both abandonment and intensification – explain this loss of breeding Ruff and indeed many other meadow birds (reviewed in Scheufler & Stiefel 1985, Beintema 1986, Zöckler 2002). Declines also spread into subarctic Scandinavia (Väisänen 2005, Väisänen *et al.* 2011, Virkkala & Rajasärkkä 2011, Øien & Aarvak 2010, Lindström & Green 2013) and to European Russia (Rakhimberdiev *et al.* 2011). The largest expanse of the current breeding range of Ruff is north of 60°N in Siberia (Lappo *et al.* 2012). Rakhimberdiev *et al.* (2011) reported that indices of abundance increased over time between the rivers Ob and Jenisej (West-Siberia), suggesting a recent global redistribution of the breeding population to areas east of the Yamal Peninsula.

A few decades ago, the estimated global population amounted to more than two million individuals distributed over a wide winter range (Zwarts *et al.* 2009). Across this range, birds from two major flyway populations occur (Stroud *et al.* 2004): a West-African population, which includes European winterers, and an East-African population, which includes Indian and South-African winterers. Several hundred thousand male and female Ruffs winter in floodplains, river sides and lakes in sub-Saharan Africa (reviewed in Cramp & Simmons 1983, Zwarts *et al.* 2009, Vervoort 2019), while fewer than 10,000 individuals, predominantly males, winter north of the Sahara, in wetlands and wet agricultural areas of the Mediterranean basin, and along the Atlantic Ocean and North Sea coasts (reviewed in Scheufler & Stiefel 1985, van Gils & Wiersma 1996).

In spring, Ruffs migrate over a broad front through Europe and Asia (OAG Münster 1989a, Wymenga 1999, Zwarts *et al.* 2009). In March–April large numbers aggregate in a few areas, usually in open landscapes with shallow water and short-sward grasslands, e.g. the grasslands in Friesland in The Netherlands (Wymenga 1999, Jukema *et al.* 2001a), the Seewinkel area in Austria (Laber 2003), the Sivash mudflats and lagoons in Ukraine (Chernichko *et al.* 1991), Hortobagy in Hungary (Kube *et al.* 1998) and the Pripyat Valley in Belarus (Karlionova *et al.* 2008). A study addressing the migratory connection between a wintering area, the Senegal Delta, and staging areas in Europe concluded that during northward migration the Senegalese winterers typically moved through the UK and The Netherlands (OAG Münster 1989a).

We studied Ruffs in an area in southwest Friesland (Verkuil & de Goeij 2003, Schmaltz *et al.* 2016), an area which is part of a major staging area for West-African Ruff in Western Europe (Wymenga 1999, Jukema *et al.* 2001a). In the study area, Ruffs largely forage in grasslands managed by dairy farmers (Verkuil & de Goeij 2003, Schmaltz *et al.* 2016, Onrust *et al.* 2017). In the 1990s the study area hosted 15–35,000 Ruffs during northward migration, but peak numbers at night roosts declined rapidly, the decline starting one year before the capture-mark-resight study (Hooijmeijer *et al.* 2010, Verkuil *et al.* 2010, 2012, Wymenga & Sikkema 2011, Schmaltz *et al.* 2015, 2016). Males start to arrive in mid-March and numbers peak in April. The majority of females appear approximately three weeks later (Jukema *et al.* 2001a); as the number of males decreases in the second half of April, the proportion of females increases (Wymenga 1999). At this stage of their annual cycle, Ruffs moult into the final breeding plumage and gain body mass (Jukema *et al.* 2001a). Stable isotope (δ13C, δ15N) measurements of primary feathers (renewed the previous year either in Europe or Africa) sampled in the Friesland in March–May (Schmaltz *et al.* 2018), suggested that 15% wintered in Europe and 75% – including all females – wintered in sub-Saharan Africa; 10% could not be assigned to a wintering area.

During 2004–2011, Schmaltz *et al.* (2015) found no support for a decline in the apparent local survival probability (i.e. the product of survival and site fidelity) of males and females. Interestingly, the analysis of apparent survival suggested that two classes of marked Ruff occurred in the study area: a high and a low-detectability class. Males in the high-detectability class had a higher apparent survival than males in the low-detectability class, a pattern which was, rather surprisingly, reversed for females. Detectability of individuals might be related to their stopover duration, visibility, or faithfulness to the study area. Warnock (2010) defined staging sites as sites "with abundant, predictable food resources where birds prepare for an energetic challenge requiring substantial fuel stores and physiological changes". Between individual heterogeneity in encounter and staying probability in a staging site has recently been observed in Red Knots *Calidris canutus* stopping over in Bohai Bay, China (Lok *et al.* 2019). In addition to variation between sites, it is therefore conceivable that between individual heterogeneity in visitation behaviour exists within sites, especially within staging sites.

Understanding how migratory species use stopover areas is important to help explain the causes of their decline (e.g. Piersma & Baker 2000, Baker *et al.* 2004). Here, we investigated within- and between-season variation in the stopover behaviour of individually marked

Ruffs stopping over in southwest Friesland during northward migration. Specifically, we described the variation in return to the study area in years after individual marking, in the timing of arrival and departure, and in minimal stopover duration. We compared males and females, which is interesting because the migratory Ruff population in southwest Friesland is heavily male biased, and it is expected that females are more sensitive to recent changes in land use in the study area and hunting in the Inner Niger Delta (Zwarts *et al.* 2009). We also considered wintering in Europe or unknown (mixed) winter origin – based on resightings and/or stable isotope measurements – as a possible source of variation. Finally, to place variation in stopover behaviour in the study area in a wider geographical context, we compared our findings with observations of individuals marked in Wommels (10 km north of the study area) and with the timing of observations of marked individuals outside the study area. Compared to previous studies based on part of this dataset (Verkuil *et al.* 2010, Schmaltz *et al.* 2015, 2016) we included additional years of fieldwork and we consider variation of individual behaviour between years. In summary, we set out to describe within- and between-individual staging behaviour of male and female Ruffs, to help understand the importance of southwest Friesland as a stopover area in a rapidly changing world.

METHODS

Study area and data collection

The study area in southwest Friesland (Verkuil & de Goeij 2003, Verkuil *et al.* 2010, Schmaltz *et al.* 2016) comprises the core of the staging area of Ruffs in Friesland, The Netherlands (Jukema *et al.* 2001a), and is located along the eastern shore of Lake IJsselmeer, between the villages Makkum (53.0566°N, 5.4039°E) in the north, Laaksum (52.8524°N, 5.4109°E) in the south, and Idzega (52.9786°N, 5.5596°E) in the east. It encompasses an area of c. 10,000 ha, of which three-quarters is covered by grasslands with monocultures of ryegrass (*Lolium* sp.) and arable land managed for the dairy industry (Groen *et al.* 2012, Howison *et al.* 2018). The study area also includes 'meadow bird reserves' where high-water tables and herb-rich grasslands are maintained (Verkuil & de Goeij 2013, Schmaltz *et al.* 2016).

Ruffs foraging in an intensively managed grassland in the study area in Southwest Friesland (photo RV, 18 April 2013).

In 2004–2012, Ruffs were caught by 'wilsternetters' using traditional methods (Jukema *et al.* 2001b, Piersma *et al.* 2005): during the day, small flocks were attracted by decoys placed on both sides of a net laying in the grass. The so-called 'wilsternet' is equivalent to a 20-m long and three meters high clap net. The catchers ringed each bird with a metal ring from the Dutch ringing scheme and measured it. Then, each individual was aged, sexed and individually marked with a unique combination of four colour rings and a coloured flag by a team from the University of Groningen (Hooijmeijer 2007). In total 6474 colour-ringed individuals were included in this study, of which 5894 (4756 males, 789 females) were captured in the study area: 349 (285 males, 64 females) between June and February and 5545 between March and May. The remaining 580 (451 males, 129 females) Ruffs were captured c. 10 km north of the study area, near Wommels (53.1064°N, 5.5875°E) and Oosterlittens (53.1359°N, 5.6495°E), and were analysed separately. Only Ruffs ringed between March and May were included in analyses of site fidelity (returning to the study area or not), whereas all 5894 Ruffs were included in analyses of arrival, departure and minimal stopover duration.

In 2005–2013, five to six observers resighted colour-marked Ruffs using a telescope. From mid-March until mid-May, six days a week, for up to 10 hours per day, observers inspected suitable foraging habitat in the morning and afternoon and visited daytime roosts during midday. The entire study area was covered approximately once every two days, trying to make the observation effort comparable between years. The flat, open landscape and the dense road network allowed observation of most flocks (Schmaltz *et al.* 2016). Resightings by members of the public and by university staff working on different projects were also included. In 2014–2019, resightings were made by a single observer (RV) from early March until late April, seven days a week, from sunrise to sunset, and the entire area was covered approximately once every five days. Because the observation schedule was different, the resightings from this period were only used to score if an individual returned (seen at least once).

To exclude possible effects of catching, handling and ringing, resightings within the season of ringing were excluded. Thus, all observations included in this study are necessarily of individuals in their second calendar year or older. Verkuil *et al.* (2010) reported a low resighting probability and a low sample size in 2005, the first year of study, and considered estimates of total stopover duration obtained in 2005 as unreliable. Therefore, resightings in 2005 were not included in analyses of arrival, departure and minimal stopover duration. Resightings outside the study area were obtained from members of the public, and from university staff visiting a site opportunistically. In the analyses we assumed that the field effort did not vary between study years. Such variation could affect the results quantitatively, but we expect that comparison between groups (female versus male, European versus mixed wintering area, transient versus staging) are less affected.

Winter origin

During early winter (October–December), colour-ringed Ruffs from southwest Friesland were resighted by observers in The Netherlands, Belgium, United Kingdom, Spain and Portugal. Assuming that Ruffs in winter are faithful to areas either north or south of the Sahara (see Kentie *et al.* 2017 for a case of an ecologically equivalent shorebird), we considered a bird as 'European-wintering' if it was either (1) observed at least once north of the Sahara during winter (n = 222) or (2) caught in the study area during winter in 2004–2012 (n = 101 individuals, 2004–2012). The remaining males were classified as of 'mixed winter origin', assuming that some might have wintered in Europe – but were never resighted (see below) or caught, while the majority probably wintered in sub-Saharan Africa (Schmaltz *et al.* 2018).

For 199 Ruffs captured and marked in March–May 2012 (187 males, 12 females), we used stable isotope measurements (δ13C, δ15N) of primary feather P9 (moulted in August–September in Europe, or October–November in sub-Saharan Africa) to classify individuals into three groups: (A) wintering in Europe (δ13C < –18.3, δ15N > 10.0), (B) of unknown winter origin (δ13C < –18.3, δ15N < 10.0) and (C) wintering in sub-Saharan Africa (δ13C > –18.3; corresponding respectively to classes A, B, and C+D in Schmaltz *et al.* 2018). Of the males in group A (n = 29), 15% were visually confirmed (based on resightings) to indeed winter in western Europe in later years, suggesting that the majority of males wintering in Europe were never resighted.

Timing of observations

For each spring between 2006 and 2013, we determined for each individual (1) arrival date (first observation in a given season; counted as 'day of year'), (2) departure date (the last observation; counted as 'day of year') and (3) minimal stopover duration in days (departure – arrival date). Thus, individuals only

observed on a single day within a season had a minimal stopover duration of zero.

We used the normalmixEM function in the R mixtools package (Benaglia *et al.* 2009) to describe the distribution of the timing of the observations of transient Ruffs and arrival and departure of staging Ruffs as a mixture of two normal distributions ($k = 2$). The mean, standard deviation and the mixing proportion (λ) of both distributions were calculated. The normalmixEM function is based on an iterative procedure with arbitrary starting values and it may give different solutions when repeated. Therefore, the calculation was repeated 1000 times and the best solution with two peaks was selected by excluding solutions which included one distribution with $\lambda < 0.1$, or with two nested peaks, and solutions were evaluated visually (see Supplementary Data for mixtools output used for visual selection). To compare the k component versus $k+1$ component fits, we used the boot.comp function in mixtools, setting P at 0.05, and testing for up to 10 components.

Classification based on minimal stopover duration: transient and staging individuals

Given that most individuals were only observed on a single day, we heuristically defined two classes of individuals: (1) 'transient' individuals, resighted only on a single day within the season, and (2) 'staging' individuals, observed on at least two different days. Due to imperfect detection, individuals may have been present before their first observation and may have stayed on for some time after their last observation, and the time between the first and last observation of an individual (minimal stopover duration) will in most cases underestimate the true stopover duration.

Consistency of individual behaviour between years

Repeatability (R; RM in Nakagawa & Schielzeth 2010) is the variance among group means (group-level variance VG) over the sum of group-level and data-level (residual) variance VR, as $R = VG/(VG+VR)$ (Stoffel *et al.* 2020). Here, individual identity – the colour code – was the grouping factor. Thus, repeatability provides a measure of how consistently individuals differ from each other. R estimation was based on mixed-effects models and its uncertainty on parametric bootstrapping (1000 repeats) using the rptR package (Nakagawa & Schielzeth 2010, Stoffel *et al.* 2020). Gaussian LMM were used to analyse arrival, departure and minimal stopover duration, and binomial GLMM to analyse presence (observed in a given season: yes/no; in the seasons up to the last season the individual was resighted), and type ('staging' versus 'transient'). The statistical significance of R was tested with a likelihood ratio test, comparing the fit of a model including the grouping factor of interest and one excluding it (Stoffel *et al.* 2020). Fixed effects were included to improve the model, but the variance associated with the fixed effects was not removed from the denominator of the repeatability equation ('enhanced agreement repeatability'; setting adjusted = FALSE; Stoffel *et al.* 2020). GLMM-based estimates of R were calculated in rptR on a latent and on the original scale; here, we present the approximations on the original scale. Because many individuals switched between staging or transient between years, analyses of repeatability were conducted by either combining all years that the individual returned, or by considering staging or transient years separately.

To investigate consistency of individuals returning more than one year after the year of capture, we also analysed date of arrival, departure and minimal stopover duration standardized within year with a LMM, including the 'number of years elapsed since the first year of observation' and wintering area as fixed effects, and individual identity as random effect.

Statistical analysis

All analyses were conducted using the statistical software R v. 3.6.1 (R Development Core Team 2008). We analysed the distribution of a variable using the fitdist and gofstat functions of the package fitdistrplus v. 1.0.11 (Delignette-Muller & Dutang 2015). We calculated linear models (LM) and generalized linear models (GLM) with the package nlme (Pinheiro *et al.* 2013) and linear mixed-effect models (LMM) and GLMM with the package lme4 v. 1.1.14 (Bates *et al.* 2015). We determined the significance of an effect for LMMs with a likelihood ratio test by comparing a full model including fixed and random effects with a null model without the effect of interest.

Because it is conceivable that staging behaviour changes with age and that fewer birds with older marks may have been present in the first years of the study, also given that the age of most birds was not known, we included the number of seasons elapsed since the season of ringing as a fixed factor in all models. To correct for repeated sampling of the same individual between years, identity was included as a random factor in LMMs. Because GLMMs assuming a Gamma distribution including identity as a random effect did not converge, we used LMMs for the analysis of arrivals (which followed a Gamma distribution; see Supplementary Data) and departures, and a GLM for the analysis of minimal stopover duration (family: Gamma

distribution, canonical link function 'inverse'; see Supplementary Data). All test results and model summaries are given in Supplementary Data.

RESULTS

Variation in resighting of individuals by year, sex and wintering area

Of all individuals marked during the study period, 43% of males (n = 2030/4756 individuals, range between years: 37–51%) and 22% of females (n = 175/789, range across years: 12–48%) were resighted in the study area in years after ringing (difference between the sexes: Wilcoxon signed-rank test: $V = 45$, $P = 0.004$). The proportion increased over the study period for males (effect of year of ringing: $\chi^2_1 = 5.7$, $P = 0.02$; average 1.4% annually), but not for females ($\chi^2_1 = 0.50$, $P = 0.5$).

Most of the marked individuals that were resighted in the study area in years after ringing were not seen each year (Figure 1, S1). Of all marked males known to be alive (because they were seen in a later year), 62% (3063/4912 individuals × years) were observed, while 52% of the females that were alive were observed in a given spring season (217/418 individuals × years). Of the males known to be alive, 58% (1257/2149) were observed in the first year after being ringed, 29% (384/1342) in the first two and 19% (137/709) in the first three years. For females known to be alive, 53% (96/181) were observed the first year, 12% (12/103) the first two years and 1% (6/65) the first three years after being ringed.

Among Ruffs resighted within a season (2006–2013), 51% of males (1516/2941, range between years 40–55%) and 79% of females (170/210, range between years: 60–87%) were observed for one day (difference between the sexes: Wilcoxon signed rank test: $V = 36$, $P = 0.008$). The proportion of such transient individuals declined over the study period in both sexes (males: $\chi^2_1 = 13.5$, $P = 0.0002$, average: –1.7% annually; females: $\chi^2_1 = 5.4$, $P = 0.02$, –3.2% annually). In males, the proportion of transient individuals increased with years after ringing ($\chi^2_1 = 13.5$, $P = 0.002$; ring ages 1–7 with $n \geq 20$). The proportion of transient females did not change with years after ringing ($\chi^2_1 = 3.0$, $P = 0.08$; ring ages 1–4 with $n \geq 20$).

Among transient male Ruffs, 5.7% (67/1516, range: 2.7–12.8%) were known to winter in Europe, whereas 15.2% of the staging Ruffs (218/1425, range: 10.4–19.7%) wintered in Europe (difference between transient and staging individuals: Wilcoxon signed-rank test: $V = 0$, $P = 0.008$). The proportion of Ruffs wintering in Europe declined in the course of the years for both classes of males (transient: average –0.7% annually, $\chi^2_1 = 6.9$, $P = 0.009$; staging: average –1.0% annually, $\chi^2_1 = 9.3$, $P = 0.002$; Figure 2B). Moreover, the proportion of individuals detected in Europe in winter at least once decreased in successive ringing cohorts (–0.3% annually, average: 3.9%, range: 2.0–5.7%; 186/4756; $\chi^2_1 = 6$, $P = 0.01$; Figure S2). The majority of European wintering males were resighted in The Netherlands (55%, 117/214), Belgium (21%, 45/214) and the United Kingdom (12%, 25/214) (Table S1).

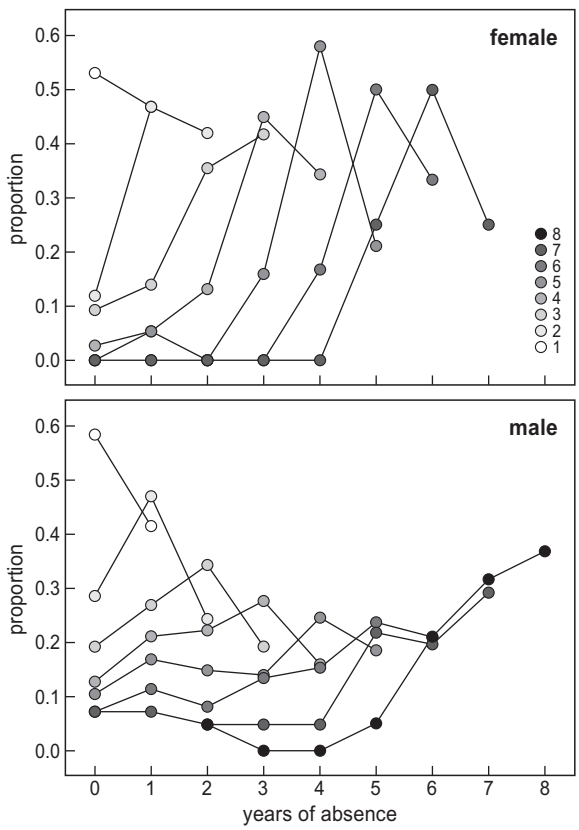

Figure 1. Proportion of Ruffs skipping spring seasons in southwest Friesland (years of absence), for eight cohorts separated by number of years after ringing (eight cohorts by ring age 1–8, shades of grey). Among females, most individuals with high ring age skipped most years before they were last seen; whereas among males the proportion of long-lived individuals skipping few years was higher, and there was higher between individual variation. Cohort sizes were, for males 2149 (for 1 year), 1342 (2), 709 (3), 368 (4), 182 (5), 97 (6), 41 (7) and 19 (8), and for females 181 (1), 103 (2), 65 (3), 38 (4), 19 (5), 6 (6), 4 (7) and 1 (8) (note that an individual is included in all cohorts up to the last time it was observed, and that within each cohort the sum of proportions is 1).

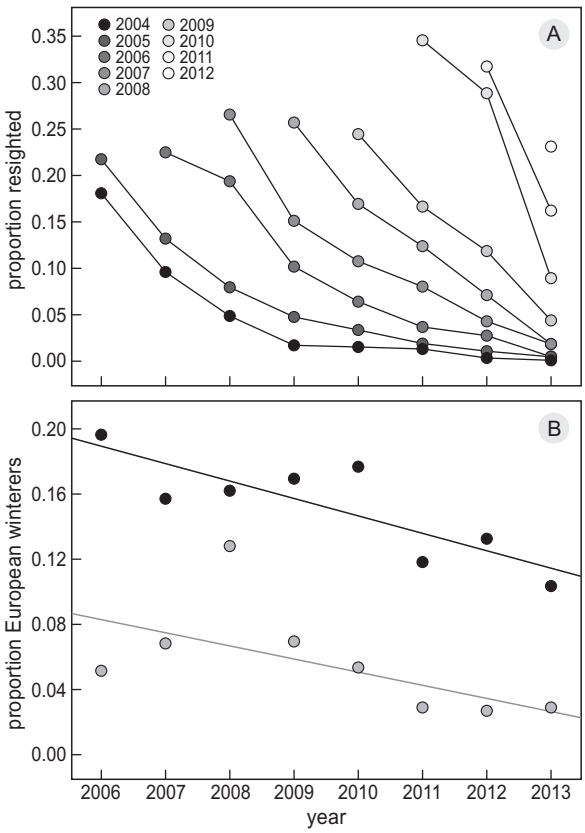

Figure 2. Between-season variation in the proportion of colour-ringed male Ruffs resighted in south-west Friesland. (A) The proportion of the males ringed in March–May 2004–2012 (year of ringing indicated by shade of grey) and resighted in 2006–2013 increased throughout the study period. The sample ringed in each year (*n*) was 979 (2004), 931 (2005), 738 (2006), 536 (2007), 420 (2008), 479 (2009), 281 (2010), 413 (2011), 420 (2012), 231 (2013). (B) The proportion of male Ruffs wintering in Europe (resighted in Europe or caught on the study site in October–December) was lower among individuals resighted in the study area in spring on a single day (transient; grey), than on multiple days (staging; black), and declined over the study period. The sample size of transient males was 212 (2006), 219 (2007), 242 (2008), 186 (2009), 203 (2010), 169 (2011), 183 (2012), 102 (2013) and of staging males 193 (2006), 184 (2007), 191 (2008), 159 (2009), 164 (2010), 177 (2011), 203 (2012), 154 (2013).

Within- and between-season variation in the timing of arrival of staging Ruffs

Staging males arrived in the study area throughout the second half of March and the first half of April, and no male Ruff was seen for the first time after 3 May. Staging females arrived on average 6.4 ± 1.8 days later than staging males (LMM: $\chi^2_1 = 12.3$, $P = 0.0004$). Arrival date of staging males advanced significantly over the study period, on average 1.0 ± 0.1 days earlier per year (LMM: $\chi^2_1 = 64.5$, $P < 0.0001$), but the effect of the number of years after ringing was not significant (LMM: $\chi^2_1 = 3.4$, $P = 0.07$; Table S5). Staging males wintering in Europe arrived on average 3.7 ± 0.8 days earlier than males of mixed winter origin (LMM: $\chi^2_1 = 18.9$, $P < 0.0001$).

European winterers that staged on the study site arrived as one cohort ($P = 0.2$; Table 1, Figure 3) with average arrival date 24 March ± 11.2 days. In contrast, staging males of mixed winter origin seemed a mixture of two cohorts ($P = 0.003$; Table 1, Figure 3), the first arriving together with European winterers (average arrival date: 23 March ± 8.1 days) and a second peak with average arrival date 6 April ± 8.5 days (normalmixEM, $\lambda = 0.65$).

Within- and between-season variation in the timing of departure of staging Ruffs

Staging Ruffs departed between late March and mid-May (Table 2). Staging females departed on average 4.5 ± 1.8 days later than males (LMM: $\chi^2_1 = 5.8$, $P = 0.02$). Among staging males, departure was independent of wintering area (LMM: $\chi^2_1 = 0.1$, $P = 0.7$) and the number of years after ringing (LMM: $\chi^2_1 = 2.1$, $P = 0.2$; Table S6). Departure date of staging males advanced over the study period, but not as strongly as for arrival date (on average 0.5 days ± 0.1 per year; LMM: $\chi^2_1 = 15.1$, $P = 0.0001$).

European winterers departed as one cohort ($P = 0.3$; Table 1, Figure 3) with an average departure date of 15 April ± 10.4 days. Males of mixed origin departed as two cohorts ($P < 0.001$; Table 1, Figure 3), leaving on average on 2 April ± 8.0 days and 19 April ± 7.4 days (normalmixEM, $\lambda = 0.70$).

Within- and between-season variation in the timing of visits of transient Ruffs

Visits of transient males advanced over the study period (0.5 ± 0.2 days per year; LMM: $\chi^2_1 = 11.3$, $P = 0.0008$). The observation date was marginally different between European and mixed winter origin transient males (European wintering transient males were on average 3.1 ± 1.4 days earlier; LMM: $\chi^2_1 = 5.1$, $P = 0.02$), and the effect of the number of years after ringing was non-significant (LMM: $\chi^2_1 = 0.7$, $P = 0.4$). The single peak of resightings of transients of European winter origin was 3 April ± 13 days ($P = 0.2$; Table1, Figure 3). The histogram of date of resighting of transient male Ruffs of mixed origin, combining all years, showed two distinct peaks ($P = 0.000$; Table1, Figure 3). This does not simply reflect variation between years, as both peaks can occur together in the same

year (Table S3), which is why it is adequate to describe their timing as a mixture of two normal distributions. The first peak of male transients occurred 28 March ± 8.7 days, whereas the second was 16 April ± 8.4 days.

Transient females visited later than transient males (average 3.6 ± 1.0 days; LMM: $\chi^2_1 = 12.3$, $P = 0.0005$). Transient females apparently migrated as one cohort ($P = 0.2$; Table 1, Supplementary Data) with a mean resighting date 9 April ± 12.9 days.

Between-season variation in minimal stopover duration

Over all seasons, 51.0% ± 5.4 of the males were seen on only one day (Figure 4). Minimal stopover duration of staging birds across the study period did not differ between the sexes (males: 17.8 ± 12.1 days for males, $n = 1423$; females: 16.1 ± 13.3 days, $n = 37$; GLM: $t = 0.9$, $P = 0.4$; Table S7). Across the study period, the minimal stopover duration of staging males varied with their wintering area (European: 20.4 ± 12.4 days; mixed winter origin: 17.3 ± 11.9 days; GLM: $t = -3.9$, $P < 0.0001$; Table S7). The minimal stopover duration increased significantly over the study period (0.4 ± 0.2 days per year, GLM: $t = -3.7$, $P = 0.0003$), but was independent of the number of years after ringing (GLM: $t = -0.55$, $P = 0.6$; Table S8).

Within-individual consistency in staging behaviour

Variables correlated with stopover behaviour showed small to moderate individual repeatability (Table 2), even after including year, age at ringing and wintering area as fixed effects (Table S9). For males returning more than one year after the year of capture ($n = 629$), variables standardized within year of observation – i.e. subtracting the mean and dividing by the standard deviation – did not change with number of years since the first observation (mean ± SD: 1.88 ± 1.14 years): arrival (LMM: $\chi^2_1 = 0.001$, $P = 1$), departure (LMM: $\chi^2_1 = 0.2$, $P = 0.7$) or minimal stopover duration (LMM: $\chi^2_1 = 0.2$, $P = 0.7$; Supplementary Data). Thus, whereas at the population level a change in date of arrival and of minimal stopover duration between years was found, our data did not support changes at the individual level.

Table 1. Timing of migration of colour-marked Ruffs in southwest Friesland. Summary statistics assuming that dates (day of year) follow a single normal distribution ($k = 1$) or a mixture of two normal distributions ($k = 2$; see Methods for details). Summary statistics by year are given in Supplementary Material.

Wintering area	Year	n	P-value*		One normal distribution		Two normal distributions						normalmixEM trials†
							Peak 1			Peak 2			
			$k = 1$	$k = 2$	Mean	SD	Mean	SD	λ	Mean	SD	λ	
Arrival (date of first observation) of staging male Ruffs													
All	All	1423	0.003	0.3	86.7	10.9	82.3	8.5	0.70	96.9	8.7	0.30	1000 / 1000
European	All	219	0.2		83.7	11.2	82.5	9.9	0.96	109.5	4.3	0.04	917 / 0
Mixed	All	1204	0.003	0.7	87.2	10.7	82.2	8.1	0.65	96.6	8.5	0.35	999 / 999
Departure (date of first observation) of staging male Ruffs													
All	All	1423	0.0	0.3	104.4	10.9	90.6	7.3	0.23	108.6	8.0	0.77	998 / 998
European	All	219	0.3		104.2	11.5	83.8	2.5	0.07	105.7	10.5	0.93	577 / 0
Mixed	All	1204	0.0	0.6	104.5	10.8	92.7	8.0	0.30	109.5	7.4	0.70	982 / 982
Date of observation of transient male Ruffs													
All	All	1517	0.0	0.03	95.8	12.6	88.0	8.9	0.58	106.6	8.2	0.42	997 / 997
European	All	93	0.2		93.3	13.0	87.8	9.5	0.75	110.3	5.2	0.25	969 / 969
Mixed	All	1424	0.0	0.03	96.0	12.6	87.7	8.7	0.55	106.1	8.4	0.45	996 / 996
Date of observation of transient female Ruffs													
All	All	170	0.2		99.6	12.9	90.0	7.8	0.54	111.1	7.1	0.46	780 / 780

n: number of different individuals. λ: mixing proportion, indicates the proportion of individuals belonging to each distribution.
*the P-value was calculated with the boot.comp function in mixtools, testing the null hypothesis of a k-component fit versus the alternative (k+1)-component fit. The most likely number of distributions is filled in grey. †the normalmixEM calculation was repeated 1000 times: the column lists how many times the selected solution was obtained and the number of meaningful solutions retained after discarding nonsensical mixtures (see Methods and Supplementary Material).

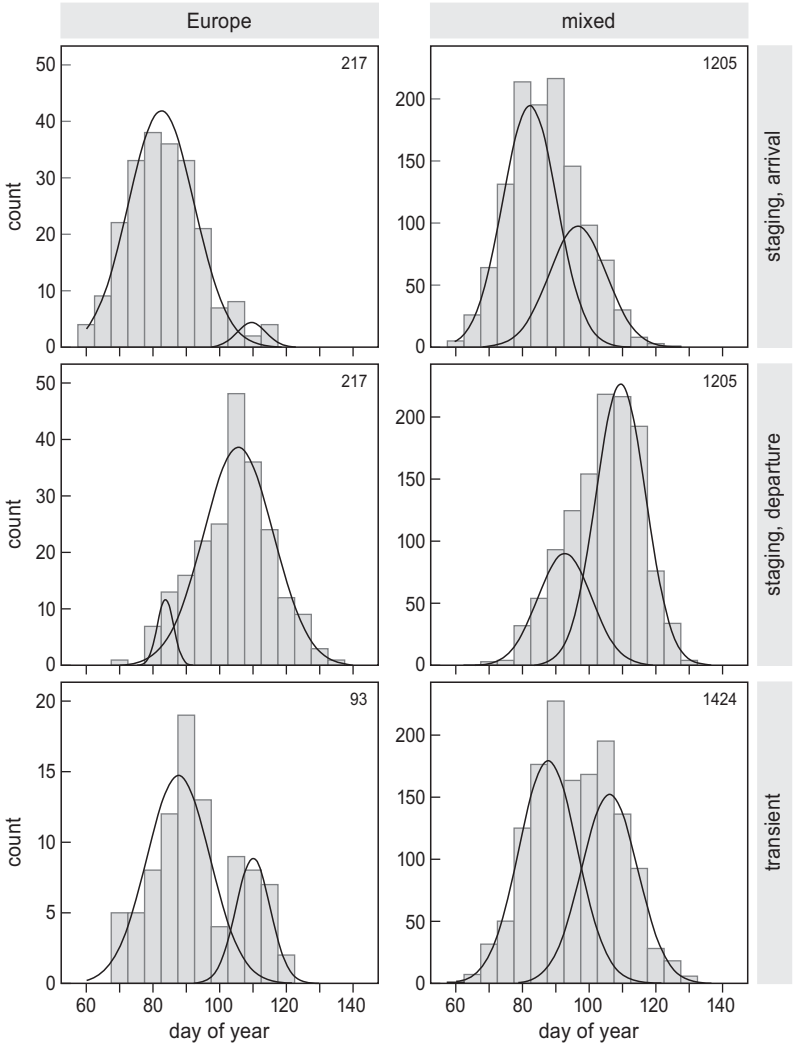

Figure 3. Fitting two normal distributions, to date of arrival and departure of staging males, and date of observation of transient males, by wintering area (Europe or mixed). The mixture of two normal distributions was calculated with the normalmixEM function of the mixtools package. The number in each panel indicates the sample size.

Table 2. Individual between-season repeatability (*R*) in aspects of staging behaviour.

Dependent variable	Sex	Group	*n*	*R* ± SE	95% CI	*P*
Resighted (No/Yes)*	M	all marked individuals	2157	0.091 ± 0.013	0.037 – 0.091	<0.0001
Type (transient versus staging)*	M	staging & transient	629	0.174 ± 0.029	0.070 – 0.179	<0.0001
Arrival date§	M	staging & transient	629	0.206 ± 0.029	0.150 – 0.262	<0.0001
	M	staging	488	0.190 ± 0.046	0.101 – 0.278	<0.0001
	M	transient#	439	0.154 ± 0.059	0.043 – 0.280	0.007
	F	transient#	25	0.141 ± 0.163	0.000 – 0.539	0.2
Departure date§	M	staging & transient	629	0.209 ± 0.030	0.152 – 0.264	<0.0001
	M	staging	488	0.175 ± 0.044	0.085 – 0.257	<0.0001
Minimal stopover duration§	M	staging & transient	629	0.255 ± 0.030	0.191 – 0.312	<0.0001
	M	staging	488	0.122 ± 0.044	0.031 – 0.205	<0.0001

n: number of different individuals. † Resighted 2005–2019 (2006–2013 for the other variables). *binomial GLMM, original-scale approximations shown. §LMM. #date of observation of transients: arrival and departure on the same day.

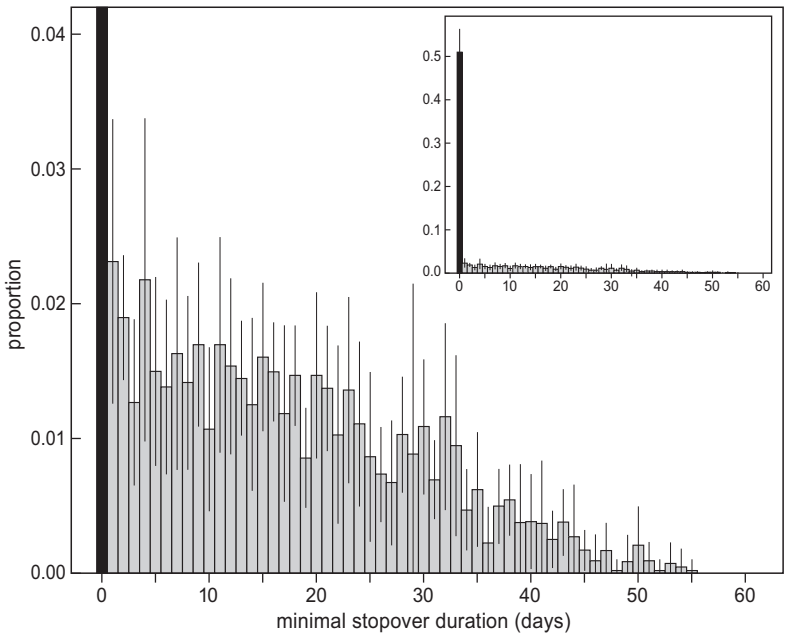

Figure 4. Transient and staging males in southwest Friesland. Minimal stopover duration of male Ruffs in southwest Friesland during the spring of 2006 to 2013. The frequency distribution showing average proportions for 2006–2013, for transient males (inset; minimal stopover duration zero; black) and staging males (light grey). Error bars represent standard deviations.

Staging behaviour and winter origin based on primary feather isotope class

Of the 199 individuals classified in 2012 on the basis of primary feather δ13C and δ15N characteristics (class A–C), 21.4% of males (40/187) but no females were resighted in the study area in 2013 (Table 3). The proportion of Ruffs wintering in Europe that returned was significantly higher (41.4%, 12/29 males of class A) than the return rate of sub-Saharan winterers (class *C*, 19%, 28/149; $G_1 = 4.6$, $P = 0.03$). Both classes had similar first and last observation dates, and hence there was no difference in minimal stopover duration (Kruskal-Wallis test: $\chi^2_1 = 1.4$, $P = 0.2$). The proportion of transient males (versus staging) was higher in sub-Saharan winterers, but the difference was not significant (25%, 3/12 of males of class A; 46% 13/28 males of class C; Fisher's exact test: $P = 0.3$).

Resightings outside the study area

Of 440 resightings of males outside the study area between 1 March – 15 May 2005–2013, 35% were also sighted in the study area in the same season (Table 4). The majority (63%) were observed in The Netherlands, including 66% of individuals also sighted in the study

Table 3. Comparison of behaviour of individual males wintering in different regions, based on feather isotope analysis (see Methods).

Group	Variable	Wintering area (class)		*P*
		Europe (A)	Sub-Saharan Africa (C)	
All marked	Number marked	29	149	
	Proportion returning	0.41	0.19	0.03
All returning	Arrival date*	92.2 ± 11.7	95.5 ± 11.5	0.40
	Departure date*	107.7 ± 11.2	105.2 ± 9.7	0.50
	Minimal stopover duration*	15.4 ± 13.4	9.6 ± 12.8	0.20
Returning, staging	Proportion of returning	0.75	0.54	0.30
	Arrival date*	88.0 ± 8.2	89.2 ± 9.4	0.80
	Departure date*	108.6 ± 11.3	107.2 ± 9.9	0.80
	Minimal stopover duration*	20.6 ± 12.0	18.0 ± 12.4	0.60
Returning, transient	Observation date	105 ± 12.5	102.8 ± 9.4	0.70

*Mean ± SD

area in the same year. Some individuals were observed in Switzerland (n = 3), Austria (n = 2), Hungary (n = 4) and Belarus (n = 1), but none of those were resighted in the study area in the same season. This was expected on the basis of the hypothesis that some individuals use an alternative eastern migratory route in some years (Verkuil *et al.* 2012). Of nine marked individuals resighted in south-eastern Europe (Switzerland, Hungary, Austria), three were females, which was a higher fraction than those resighted in western Europe (39/434; Fisher's exact test: P = 0.02).

Arrival date of marked males outside the study area varied significantly with latitude (Figure 5; LMM: χ^2_1 = 145, $P < 0.0001$) and was significantly earlier for European winterers (LMM: χ^2_1 = 35, $P < 0.0001$). The model included individual identity and year as random effects (see Supplementary Data).

Behaviour of males ringed outside the study area

Among the individuals marked north of the study area (in Wommels, n = 451), 64% used the study area for a single day stopover, rather than for staging, compared to 52% of individuals marked in the study area (Table S10). The proportion of males that was never resighted in later years was similar for both ringing locations, and those that were resighted had similar timing of their visits (Table S10; Supplementary Data).

DISCUSSION

Southwest Friesland is one of the most important staging areas in western Europe for Ruffs during northward migration (Wymenga 1999), but from 2002 onwards the peak numbers counted at night roosts

Table 4. Arrival date of marked Ruffs outside the study area, and proportion that were also observed in the study area in the same season, and their arrival day in the study area. Ruffs were caught and colour-ringed in 2004–2012 and resighted between 1 March and 15 May in 2005–2013. Individuals resighted multiple times in the same season in the same area were included only once.

Country	Males				Females			
	Outside the study area		In the study area		Outside the study area		In the study area	
	n	Mean arrival day	Proportion resighted	Mean arrival day	n	Mean arrival day	Proportion resighted	Mean arrival day
All	440		0.35		31		0.06	
Senegal	1	136 (15 May)	0.00					
Morocco	1	80 (21March)	0.00					
Spain	2	76 (17 March)	0.00		2	85 (26 March)	0.00	
Portugal	4	80 (21March)	0.50	96 (6 April)				
Italy	6	75 (16 March)	0.17	104 (14 April)				
France	15	72 (13 March)	0.20	83 (24 March)	3	114 (24 April)	0.00	
Belgium	30	71 (12 March)	0.47	96 (6 April)	2	75 (16 March)	0.00	
United Kingdom	17	73 (14 March)	0.29	91 (1 April)				
The Netherlands	276	103 (13 April)	0.35	90 (31 March)	18	107 (17 April)	0.11	91 (1 April)
Germany	8	112 (22 April)	0.38	83 (24 March)	1	125 (5 May)	0.00	
Denmark	19	114 (24 April)	0.53	91 (1 April)				
Poland	2	124 (4 May)	0.00					
Lithuania	6	119 (29 April)	0.33	104 (14 April)				
Estonia	2	126 (6 May)	1.00	95 (5 April)				
Sweden	33	127 (7 May)	0.33	93 (3 April)	1	129 (9 May)	0.00	
Finland	7	127 (7 May)	0.43	101 (11 April)	1	126 (6 May)	0.00	
Norway	4	127 (7 May)	0.50	80 (21 March)				
Austria	1	116 (26 April)	0.00		1	116 (26 April)	0.00	
Hungary	2	110 (20 April)	0.00		2	104 (14 April)	0.00	
Switzerland	3	96 (6 April)	0.00					
Belarus	1	117 (27 April)	0.00					

n: the total number of individuals resighted outside the study area (by country).

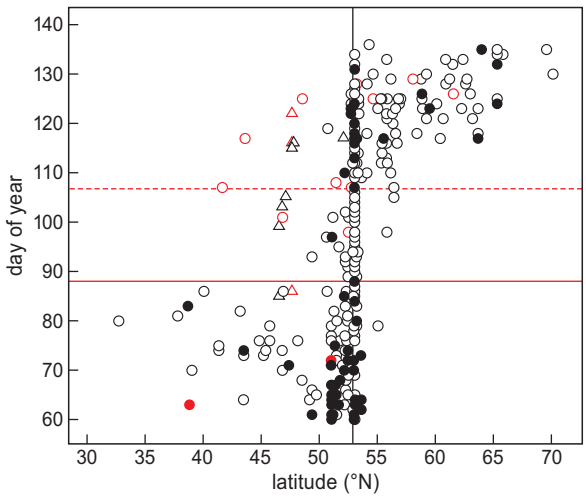

Figure 5. Northward migration of marked Ruffs in Western Europe. First observation (arrival) of marked individuals resighted outside southwest Friesland, 1 March – 15 May 2005–2013. Filled symbols: European winterers – resighted in Europe in October – December. Open symbols: mixed winter origin. Triangles: southeast of Europe (Austria, Hungary, Switzerland). Black: males; red: females. Red horizontal lines indicate the mean first (solid) and second peak (dotted) of observations of transient males in southwest Friesland. The black vertical line indicates the latitude of the study area.

along Lake IJsselmeer steeply declined, with a decrease of 22.4% per year between 2004 and 2013 (own unpubl. data). To help explain the causes of the decline, and to examine whether this affected some types of individuals more than other (Schmaltz *et al.* 2015), we studied variation in the timing and duration of visits in this area using a capture-mark-resight approach. We found high heterogeneity in visiting behaviour, with a large proportion of marked individuals never seen again in years after ringing, and a large proportion being observed a single day (transient) rather than longer (staging). At the population level, between-year changes in our measures of staging behaviour (skipping years, arrival, departure, minimal staging duration) were small compared with high within-individual variation. The proportion of individuals that returned was lower for females than for males, and females were also more likely to be classified as transient. Marked females migrated later than males, but less than the three weeks expected from field observations of unmarked birds (Jukema *et al.* 2001a). Compared with sub-Saharan winterers, European winterers were more likely to return to the study area, and more likely to stage rather than be transient. We discuss the spring migration strategy of Ruffs in Western Europe based on the occurrence and timing of two waves of transients, the timing of resightings of marked individuals outside the study area, the timing of resightings of individuals marked in Wommels and of spring migration in Europe.

Heterogeneity of the migratory population

A large proportion of migrant Ruffs (51% of males and 71% of females) visited the study area only briefly. The 51.0% of males seen only on one day is much higher than expected from the distribution of minimal stopover duration of the males that were observed on at least two days in a given season (expected 1.30% ± 0.04 males seen only one day, based on 1000 simulations assuming a Gamma distribution with observed shape = 1.6 and rate = 0.09). Because the proportion of individuals seen only on a single day was much higher than expected (Figure 4), we used this visit duration as a cut-off to distinguish between two types of visitors: transient and staging individuals. Warnock (2010) defined staging sites as special stopover sites where migrants typically make longer stops (weeks), have a higher refuelling rate and prepare for a longer flight (Piersma 1987). Thus, the study area in southwest Friesland could be considered a staging site, hosting a mixture of staging and transient Ruffs. Similar within-site heterogeneity was recently reported in *Calidris canutus piersmai* staging in Bohai Bay, China, during spring migration (Lok *et al.* 2019).

Heterogeneity of stopover duration described here probably contributes to the occurrence of two detectability classes in the Ruff population in southwest Friesland (Schmaltz *et al.* 2015). In that study, implementing the probability of membership to the high (π_{HD}) and low detectability (π_{LD}) class was crucial to achieve fits of data with survival models. Based on a Ruff being resighted in a season or not, π_{HD} and π_{LD} were assigned to individuals for their lifetime. As we show here, the behaviour of individuals is not highly repeatable but varies between years. This prevents direct comparisons between the two studies.

Timing of Ruff migration in southwest Friesland

OAG Münster (1994) found that northward migrating Ruffs occurred later at more northerly sites. The study suggested that at least part of the population makes more than one stop when crossing inland Europe. This was later supported by stable isotope analysis (δ13C, δ15N) of blood, indicating that most individuals visiting southwest Friesland had already arrived in Europe several weeks before showing up in Friesland (Schmaltz *et al.* 2018). Here, we report that the arrival

of marked male Ruffs in Western Europe was significantly later with increasing latitude, again in line with the findings of OAG Münster (1994). As expected for Ruffs migrating along the westernmost route, the mean arrival of marked males in countries south-west of the study area (including Italy) preceded the mean arrival in The Netherlands, whereas north-eastern countries were visited later (Table 4, Figure 5). In the first half of April, the vast majority of marked males were seen between 51° and 54°N (Figure 5).

In southwest Friesland, the timing of observations of transient males typically showed two peaks (means: 28 March and 16 April), coinciding with arrivals (mean: 27 March; Wilcoxon signed-rank test: $V = 9$, $P = 0.2$) and departures (mean: 14 April; Wilcoxon signed-rank test: $V = 14$, $P = 0.6$) of staging males. Although both peaks occurred irrespective of winter origin, the single distribution was favoured for European winterers (Table 1, Figure 3). We will now discuss the biological meaning of fitting two distributions for males of mixed winter origin in the context of the timing of Ruff migration in Western Europe. North of the study area, most Ruff flocks arrive only in late April – early May (see Wymenga 1997a, 1999, Meltofte & Clausen 2016). Even in the German and Danish Wadden Sea, c. 200 km northeast of southwest Friesland, Ruff numbers do not increase before the second half of April and peak in early May (Laursen *et al.* 2010). In agreement with these counts, marked individuals were only rarely reported north of 54°N before the second peak (Figure 5). Thus, it is unlikely that Ruffs of the first peak leave The Netherlands before mid-April, and therefore they probably stage just outside the study area (see Wymenga 2005 for areas). Two lines of evidence support the notion that extensive exchange between the study area and nearby areas occurs. First, Ruffs marked near Wommels, c. 10 km north of the study area, visited the study area in later years at similar times to Ruffs ringed in the study area (Table S10). Second, 35% of marked Ruffs resighted in The Netherlands outside the study area were also seen in the study area in the same spring (Table 4).

The second period of increased observation of transients coincides with the build-up of Ruff numbers (e.g. Laursen *et al.* 2010 and Meltofte & Clausen 2016) as well as an increase in the number of observations of marked Ruffs northeast of The Netherlands (Figure 5). In 1997, Wymenga (1997b), noting the increased mobility of Ruffs starting from 21 April within Friesland, interpreted this as local movements or arrival of new migrants. Remarkably, no marked male Ruffs arrived in southern Europe during the second peak (Figure 5), indicating that this second wave largely consists of males which were already north of 51°N before the end of March. In summary, the two peaks of transient males may reflect two periods of increased mobility of individuals staging between 51° and 54°N after (early peak) or before (late peak) stopping-over in the study area, whereas Ruffs staging in southwest Friesland arrived with the first and departed with the second wave. The mixture of arrivals (mean 23 March and 6 April) and departures (mean 2 and 19 April) of staging males of mixed wintering origin may explain the shape of the distribution of their minimal stopover durations (Figure 4), which fits a gamma distribution better than a normal distribution.

Individual repeatability of arrival, departure and minimal stopover duration was relatively low (≤ 0.25; Table 2, S9) compared to values calculated for other migratory bird species (generally > 0.30 and up to 0.92; see Table 1 in Both *et al.* 2016), indicating that returning individuals were not particularly consistent between years. Staging and transient males did advance their arrival in the study area at the population level, but no consistent within-individual change was detected for males that returned in multiple years (Figure S7A). A possible explanation for this discrepancy could be the relatively brief life-spans of most individuals (2.0 ± 1.2 years between first and last returning year). Alternatively, individual Ruffs may not advance their arrival as they age, but the advanced arrival at the population level may be due the earlier arrival of cohorts ringed in more recent years. A similar discrepancy between population and individual advancement of spring arrival was observed in Black-tailed Godwits *Limosa limosa islandica* in Iceland, which was explained by earlier arrival of new recruits to the population (Gill *et al.* 2014).

Comparison between winter origins

The majority of Ruffs staging in Friesland winter in sub-Saharan Africa (Schmaltz *et al.* 2015), in the seasonal floodplains along the lower Senegal River and the Inner Niger Delta in Mali (Zwarts *et al.* 2009). After 2000, only few Ruffs remained in the Senegal Delta (Triplet *et al.* 2014). Thus, during our study, most sub-Saharan Ruffs visiting Friesland must have wintered in the Inner Niger Delta, from where population trends are unknown. The timing of staging Ruff of mixed wintering areas was less homogeneous than that of European winterers: for mixed wintering areas we observed a second cohort arriving ca. two weeks later, and a second cohort departing ca. two weeks earlier than the main cohort. As discussed above for tran-

sients, staging males leaving earlier probably stay at nearby sites in Friesland before migrating northward.

Of all males marked in spring 2004–2012, 3.9% were resighted in Europe in winter, predominantly in The Netherlands, Belgium and the United Kingdom (Table S4, Figure S2). Their higher proportions among staging (15.2%) and transient males (5.7%) indicated that European winterers were more likely to return to the study area than sub-Saharan winterers, and were more likely to stage than be transient. These proportions declined by 1.0% and 0.7% per year, respectively (Figure 2B). Does this indicate that European winterers have been in even steeper decline than sub-Saharan winterers?

The small population wintering in France was stable in 1980–2013 and increased thereafter (Quaintenne *et al.* 2015, Schmaltz *et al.* 2019). Ruffs increasingly wintered in the United Kingdom in the 1950s and 1960s (Prater 1973) and up until c. 2005, but during the study period, short-term trends were negative (Austin *et al.* 2014); the annual index of wintering Ruffs declined from c. 200 at the beginning of the millennium, to c. 100 after the winter 2004–2005 (Frost *et al.* 2020). In the 1970s and 1980s the number of Ruffs wintering along the border in Belgium and The Netherlands increased (Castelijns *et al.* 1988). Wintering in Belgium declined by 1.8–17.2% (average: ≤ 5%) annually between 2003–2004 and 2012–2013 (Devos & Onkelinx 2013). Interestingly, in Belgium counts of c. 2500 individuals were frequent until the winter 2006–2007, after which counts were much lower (Devos & Onkelinx 2013). In The Netherlands, Ruff winter numbers have also declined between 2002–2013 (average 5% per year; Figure S3) and, similar to Belgium and the United Kingdom, most birds were lost in the middle of the decade.

To conclude, to explain their decreasing proportion in the marked migratory population (Figure 2B), the decline of European winterers was probably not large enough, i.e. lower than the 8–22% decline of the largest European breeding populations (Øien & Aarvak 2010, Rakhimberdiev *et al.* 2011, Laaksonen & Lehikoinen 2013, Lindström & Green 2013, Lindström *et al.* 2019). An alternative explanation could be an observer effect, i.e. a decrease of the reporting rate of marked individuals in Europe. This explanation has merit as the proportion of marked males resighted in Europe in winter (3.9%) was lower than the 17.5% expected from the feather isotope analysis (Fisher's exact test: $P < 0.0001$), indicating that the majority of colour-ringed males remained undetected in Europe. Furthermore, the proportion of individuals ringed in a given year that were observed in winter in Europe declined over time (Figure S2).

Comparison between females and males

The Frisian migratory population largely consists of males (Jukema *et al.* 2001a). Jukema *et al.* (2001a), calculating the number of females across the season based on the sex-ratio in catches and roost counts, concluded that female migration peaked three weeks later than male migration, resulting in an increased proportion of females from mid-April onwards (Jukema *et al.* 2001a, Verkuil & de Goeij 2003). This agrees with a three-week delay in departure of females from the African winter grounds (Zwarts *et al.* 2009). In inland Germany (OAG Münster 1989b, 1990) and Eastern Europe (Wymenga 1999) the proportion of females in migratory flocks was higher, but their timing of migration was similar to the females in Friesland (OAG Münster 1989b). Data on arrival of marked females in western Europe is in line with these studies: most marked females resighted south of 51°N were of unknown winter origin and seen after the first peak of transient males (Figure 5).

Resightings of marked females in the study area, however, was not consistent with the idea that females migrate three weeks later. Staging females arrived on average only 6.5 days later and departed on average 4.5 days later than males, and the difference between the early and late peak of transient males and females was only 2.0 and 4.5 days, respectively. This discrepancy may be resolved by an overrepresentation of females wintering in the United Kingdom, Belgium and The Netherlands (north of 51°N) among returning females, and therefore also among marked females studied here. Support for this view comes from the observation that females known to winter in Europe were more likely to be resighted in the study area (8 of 17 individuals) than females of mixed wintering areas (154 of 772 individuals; Fisher's exact test: $P = 0.01$), and more likely to be staging versus transient (8 of 18 bird years) than females of mixed wintering areas (29 of 189 birds × years; Fisher's exact test: $P = 0.006$).

More marked females (78%) than males (57%), were never resighted in the study area in the years after ringing. These proportions exceed the proportion of first-year Ruffs in the winter population (e.g. 22.7% in Zwarts *et al.* 2009 and 23.8–31.2% in OAG Münster 1996) and the 22.4% annual decline of the staging population. Low resighting proportions may be explained by a combination of low site fidelity, missed observations during brief stopovers and low true survival. Sex-specific habitat preferences of migratory Ruffs (Verkuil

& de Goeij 2003), in particular a more pronounced preference by females for grasslands with higher water tables, predict that females would be more sensitive to recent habitat changes. Females may also suffer disproportionate losses due to human hunting in the Sahel, because hunting pressure increases late in the season and females depart later (Zwarts *et al.* 2009). The decreasing proportion of females in the catches in Friesland over the years (Schmaltz *et al.* 2015) fits with this prediction. Thus, low winter season survival of females may contribute to their low return rates.

Among birds that were resighted, many were not seen every year. In fact, in all the years individuals were known to be alive, i.e. before their last resighting in the study area, they were not observed in 38% (males) and 48% (females) of cases. Among resighted birds, the proportion of individuals seen consistently each year dropped with age after ringing in both sexes (Figure 1, S1). Among marked individuals resighted outside the study area between 1 March and 15 May, only 38% of males and 6% of females were resighted in the study area in the same year, suggesting that staging site infidelity or missing local observations indeed occur (Table 4). Marked individuals that were not seen in a given spring may have taken a different migratory route (see Verkuil *et al.* 2012). This could be the case for individuals resighted in south-eastern Europe (Switzerland, Austria, Hungary) where spring phenology is comparable to Friesland (Laber *et al.* 2003), and for the those resighted east of the study area (Belarus), although spring passage is later there (Verkuil *et al.* 2012). Despite the small sample size, the significantly higher proportion of females resighted in south-eastern Europe suggested that lower stopover site fidelity may indeed contribute to lower return rates of females.

Changes between years in the stopover population

Between 1975 and 2000 the number of Ruffs on night roosts along Lake IJsselmeer increased by 260%, presumably because new roosting islands were created along the lake shore (Hooijmeijer *et al.* 2010). This suggests that the habitat was still adequate for migratory Ruffs, in particular for males (Verkuil & de Goeij 2003). Following this increase, during the study period (2004–2013), the migratory population along the lake severely declined at a constant rate of 22.4% per year (own unpubl. data). In the years following our study, the population staging in the entire province continued to decline (Wymenga *et al.* 2020). Ongoing intensification of dairy farming, with lowering water tables, reduced grazing and more frequent reseeding with single grass varieties (Kleijn *et al.* 2009, 2010, Vickery *et al.* 2001, Schroeder *et al.* 2012, Kentie *et al.* 2013), lead to the disappearance of the surfacing 'red' earthworm species eaten by Ruffs during daytime (Onrust *et al.* 2017, 2019). This may have contributed to a reduction of the feeding opportunities for migratory Ruffs. From 2001 to 2008, the decline was paralleled by a decrease in daily body mass gains (Verkuil *et al.* 2012), which in comparison with mass changes in the Pripyat Valley in Belarus, was interpreted to be a consequence of changing habitat quality in the Dutch study area due to changing dairy farming practices.

The minimal stopover duration of returning individuals increased by 0.4 days/year, the proportion of individuals that staged (versus transients) increased by 1.7% per year for males and 3.2% for females and the proportion of individuals that were never seen again decreased by 1.4% per year for males. Taken together, these trends should lead to an increase rather than a decrease in the numbers at night roosts. Possible causes for the gradual change in stopover dynamics remain speculative. In view of the stopover scenario outlined above, southwest Friesland is part of a larger region used by migratory Ruffs, and gradual shifts of spatial preferences may have generated the variability between years. In concert with the reduced population size, the occurrence of marked Ruffs became restricted to a smaller area in southwest Friesland, concentrating close to the main night and daytime roosts (Schmaltz *et al.* 2016). Based on night roost counts, Wymenga (1997b) suggested an increasing preference for the IJsselmeer coast over inland locations in the 1990s, whereas in the 2000s (Wymenga 2005) and in 2015–2019 inland roost counts increased again (Wymenga *et al.* 2020). These shifts may be driven by changing local conditions such as of the creation of new night roosts (Hooijmeijer *et al.* 2010) or daytime roosts (Schmaltz *et al.* 2016), changing water levels (Wymenga 1997b), an increasing presence of aerial predators (Piersma *et al.* 2003) or changing management of nature reserves.

Final reflection

Our study of Ruffs during migration through southwest Friesland has shown that the picture of a uniform staging population moving-in from the south and moving-out to the north, with some individuals being early and others late, but with population averages characterizing individual timing (e.g. Piersma & Baker 2000) does not hold up. The view of a uniform staging population seems to fit the observations on tundra-breeding Bar-tailed Godwits *Limosa lapponica* refuelling on the intertidal areas in the very near, but ecologically totally distinct, Wadden Sea (Piersma & Jukema 1990,

Rakhimberdiev *et al.* 2017). This contrast may suggest that monogamous and site-faithful shorebird species such as Bar-tailed Godwits differ in important ways from lek-breeding species with high between individual variation in lek attachment such as Ruffs (Vervoort & Kempenaers 2019). Inspired by this and other differences (see e.g. Piersma 2003, Kempenaers & Valcu 2017), the degrees and the sources of individual heterogeneity in migration routines in closely related species with distinct reproductive and trophic ecologies, may well provide a rich source of comparisons to illuminate the role of migration in the evolution of life histories. The present study can be considered a small building block towards such an understanding.

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SAMENVATTING

Kemphanen *Calidris pugnax* die van de overwinteringsgebieden in West-Afrika en Europa naar de broedgebieden in noordelijk Eurazië trekken, maken onderweg gebruik van stopplaatsen. We bestudeerden de variatie in de timing van het individuele verblijf op een stopplaats in Zuidwest-Friesland (53°N, Nederland), op basis van 6474 Kemphanen die in 2004–2012 van kleurringen waren voorzien. Slechts 43% van de mannelijke en 22% van de vrouwelijke Kemphanen werd in maart–mei in de jaren na het ringen in het onderzoeksgebied waargenomen. De minimale verblijfsduur van terugkerende individuen varieerde aanzienlijk binnen het seizoen. We onderscheidden twee categorieën: (1) 'kort-blijvende' individuen werden slechts op één dag waargenomen in het studiegebied (51% van de waargenomen mannelijke en 79% van de waargenomen vrouwelijke Kemphanen), en (2) 'lang-blijvende' individuen, die op meerdere dagen waargenomen werden. We stelden twee seizoenspieken van waarnemingen van kort-blijvende Kemphanen vast, samenvallend met de pieken van aankomst en vertrek van lang-blijvende Kemphanen. Haantjes die in Europa overwinterden, keerden met grotere waarschijnlijkheid terug naar het onderzoeksgebied en kwamen ook eerder aan dan vogels met onbekend wintergebied (respectievelijk, 3,1 dagen en 3,7 dagen voor kort- en lang-blijvende haantjes), maar de tijd van vertrek verschilde niet tussen beide groepen. Kort- en lang-blijvende hennetjes kwamen later aan dan de haantjes. De timing van doortrek van individuen was niet consistent tussen jaren en individuen kwamen niet significant vroeger aan naarmate ze ouder werden, in tegenstelling tot de vervroeging die we op populatieniveau vaststelden. Het gegeven dat een groot aandeel van de Kemphanen dat Zuidwest-Friesland aandoet er slechts kort verblijft, doet veronderstellen dat tijdens de noordwaartse trek veel individuen afhankelijk zijn van andere stopplaatsen voor hun rui en opvetten. Waarnemingen van gekleurringde Kemphanen elders in West-Europa suggereren dat deze stopplaatsen hoofdzakelijk tussen 51° en 54°N gelegen zijn. Samenvattend kunnen we stellen dat, tijdens de voorjaarstrek de minimale verblijfsduur van Kemphanen geringd in Zuidwest-Friesland naast een grote individuele variatie ook een grote variatie tussen jaren voor eenzelfde individu vertoont.

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SUPPLEMENTARY MATERIAL

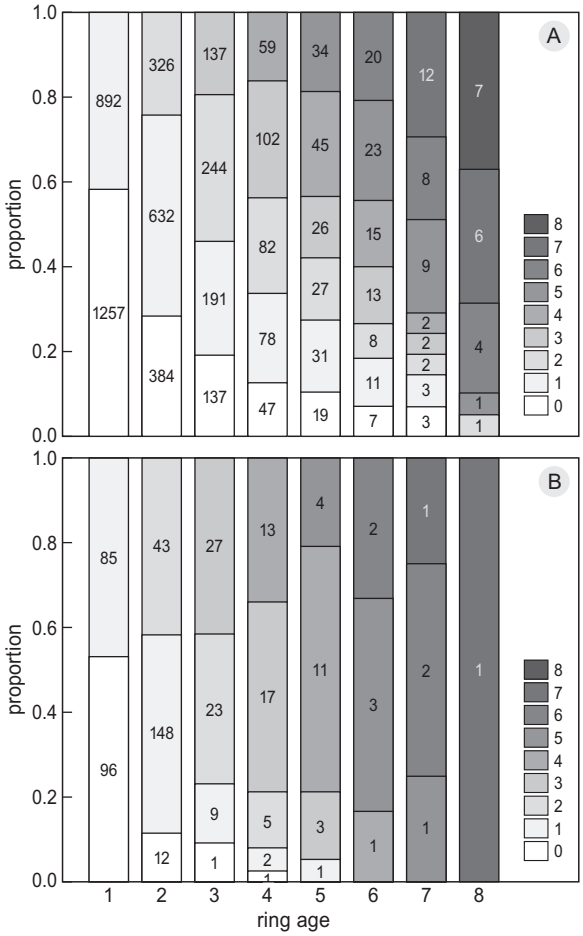

Figure S1. Proportion of (A) male and (B) female Ruffs absent for 0–8 years (shade of grey), by number of years after ringing (ring age). Sample size is given for each age.

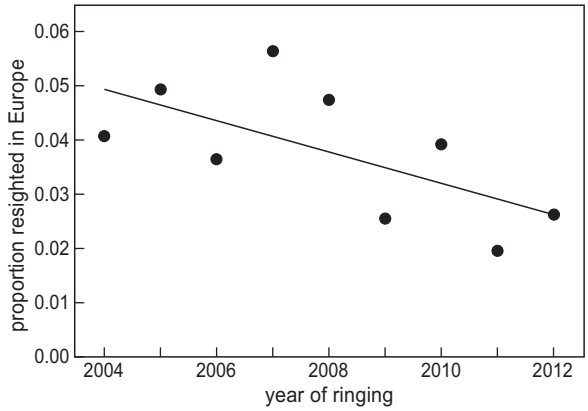

Figure S2. Proportion of male individuals known to have wintered in Europe (resighted in Europe at least once in October–December 2004–2019), by year of ringing (in March–May).

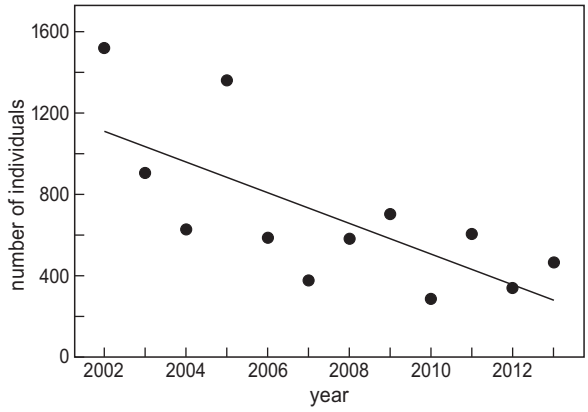

Figure S3. Maximum winter count of Ruffs in The Netherlands. For each winter, the maximum monthly count in October–December was selected (Sovon waterbird monitoring reports available at www.sovon.nl/nl/monitoringrapporten).

Table S1. Arrival (date of first observation) of staging male Ruffs. Analysis assuming that arrival dates follow a single normal distribution or a mix of two normal distributions (see Methods for details).

Wintering area	Year	n	P-value*		One normal distribution		Two normal distributions						normalmixEM trials†
							Peak 1			Peak 2			
			$k = 1$	$k = 2$	Mean	SD	Mean	SD	λ	Mean	SD	λ	
All	2006	193	0.3		92.4	9.3	89.8	7.5	0.85	106.7	4.3	0.15	268 / 268
All	2007	184	0.3		91.5	9.8	70.0	3.0	0.06	92.9	8.4	0.94	300 / 0
All	2008	190	0.8		86.9	10.3	61.3	0.44	0.04	87.8	9.2	0.96	26 / 0
All	2009	159	0.0	0.02	81.2	9.9	80.1	7.8	0.97	115.4	2.2	0.03	35 / 313
All	2010	165	0.2		87.1	11.2	84.5	9.1	0.88	106.5	4.8	0.12	952 / 952
All	2011	176	0.8		84.2	9.9	82.0	7.7	0.89	101.8	8.3	0.11	796 / 910
All	2012	202	0.0	0.1	81.0	9.0	76.7	5.4	0.63	88.4	9.2	0.37	992 / 992
All	2013	154	0.8		89.0	11.4	81.5	8.5	0.58	99.1	5.5	0.42	870 / 870

n: number of different individuals. λ: mixing proportion, indicates the proportion of individuals belonging to each distribution. *the P-value was calculated with the boot.comp function in mixtools, testing the null hypothesis of a k-component fit versus the alternative (k+1).

Table S2. Departure (date of last observation) of staging male Ruffs. Analysis assuming that departure dates follow a single normal distribution or a mixture of two normal distributions (see Methods for details).

Wintering area	Year	n	P-value*		One normal distribution		Two normal distributions						normalmixEM trials†
							Peak 1			Peak 2			
			$k = 1$	$k = 2$	Mean	SD	Mean	SD	λ	Mean	SD	λ	
All	2006	193	0.4		108.5	10.3	90.7	4.9	0.10	110.5	8.7	0.90	824 / 824
All	2007	184	0.1		107.0	10.4	103.1	9.0	0.74	118.0	4.6	0.26	794 / 794
All	2008	190	0.2		104.8	9.6	89.2	4.9	0.14	107.4	7.5	0.86	475 / 475
All	2009	159	0.0	0.6	97.7	11.8	84.7	2.4	0.22	101.3	10.8	0.78	944 / 999
All	2010	165	0.02	0.4	105.7	9.6	90.2	4.9	0.17	108.8	6.8	0.83	365 / 990
All	2011	176	0.2		104.1	10.7	100.7	9.5	0.77	115.8	4.4	0.23	768 / 876
All	2012	202	0.0	0.09	101.1	11.0	92.4	8.6	0.49	109.3	5.2	0.51	584 / 844
All	2013	154	0.05	0.6	106.3	10.0	80.2	6.8	0.04	107.6	8.3	0.96	38 / 0

n: number of different individuals. λ: mixing proportion, indicates the proportion of individuals belonging to each distribution. *the P-value was calculated with the boot.comp function in mixtools, testing the null hypothesis of a k-component fit versus the alternative (k+1).

Table S3. Date of observation of transient Ruffs. Analysis assuming that departure dates follow a single normal distribution or a mixture of two normal distributions (see Methods for details).

Wintering area	Year	n	P-value*		One normal distribution		Two normal distributions						normalmixEM trials†
							Peak 1			Peak 2			
			$k = 1$	$k = 2$	Mean	SD	Mean	SD	λ	Mean	SD	λ	
All	2006	212	0.0	0.4	99.3	11.2	91.5	6.7	0.58	107.0	3.5	0.33	124 / 174
All	2007	219	0.05		97.7	13.7	96.8	13.0	0.97	124.3	0.5	0.03	658 / 0
All	2008	242	0.2		95.7	12.1	89.5	9.6	0.65	107.3	6.3	0.35	679 / 679
All	2009	186	0.0	0.2	92.3	12.2	84.3	6.4	0.59	103.9	8.7	0.41	533 / 587
All	2010	203	0.0	0.04	96.0	11.3	88.9	7.1	0.63	107.9	5.3	0.37	655 / 950
All	2011	169	0.03	0.2	95.0	12.8	87.7	8.9	0.64	108.0	6.8	0.36	689 / 689
All	2012	183	0.007	0.3	92.1	12.3	86.6	8.8	0.74	108.1	5.1	0.26	790 / 790
All	2013	103	0.009	0.2	98.8	13.8	76.1	5.6	0.19	104.0	9.1	0.81	510 / 978

n: number of different individuals. λ: mixing proportion, indicates the proportion of individuals belonging to each distribution. *the P-value was calculated with the boot.comp function in mixtools, testing the null hypothesis of a k-component fit versus the alternative (k+1).

Table S4. Proportion of males wintering in Europe resighted by country.

Country	Proportion	Number
Belgium	0.210	45
France	0.019	4
Germany	0.014	3
Portugal	0.042	9
Spain	0.051	11
The Netherlands	0.547	117
United Kingdom	0.117	25

Table S5. Date of arrival of staging males, by number of seasons since ringing (ring age).

Ring age	Number	Median	Mean ± SD
1	601	87	87.7 ± 10.9
2	406	87	87.2 ± 10.7
3	210	83	85.2 ± 11.1
4	109	82	84.2 ± 10.1
5	55	83	82.7 ± 11.2
6	29	85	85.1 ± 10.1

Table S6. Date of departure of staging male Ruffs, by number of seasons since ringing (ring age).

Ring age	Number	Median	Mean ± SD
1	601	106	104.6 ± 11.1
2	406	107	105.4 ± 10.5
3	210	105	103.9 ± 11.5
4	109	104	102.5 ± 9.8
5	55	104	102.8 ± 11.7
6	29	106	104.9 ± 9.9

Table S7. Minimal stopover duration of staging Ruffs.

Sex	Wintering area	Year	Median	Mean ± SD
all	all	all	16	17.8 ± 12.1
female	all	all	14	16.1 ± 13.3
male	Europe	all	19	20.4 ± 12.4
male	mixed	all	15	17.3 ±11.9
male	all	2006	15	16.1 ± 11.5
male	all	2007	14	15.5 ± 11.2
male	all	2008	16	17.9 ± 11.5
male	all	2009	15	16.5 ± 12.4
male	all	2010	16	18.6 ± 12.5
male	all	2011	19	19.9 ± 11.8
male	all	2012	18	19.9 ± 11.9
male	all	2013	14	17.4 ± 13.5

Table S8. Minimal stopover duration of adult males by number of seasons since ringing (ring age).

Ring age	Number	Median	Mean ± SD
1	601	15	16.9 ± 11.5
2	406	16	18.2 ± 12.1
3	210	16	18.7 ± 13.1
4	109	17	18.3 ± 11.8
5	55	19	20.1 ± 13.2
6	29	19	19.7 ± 12.1

Table S9. Repeatability of individual timing, including fixed effects year, ring age and wintering area.

Dependent variable	Sex	Class	Effect	*R*	CI	*P*
Resighted or not (N/Y)[†*]	M	not seen & staging & transient	individual (n = 2157)	0.068 ± 0.006	0.039 – 0.060	<0.0001
			year, ring age, wintering area	0.014 ± 0.003	0.010 – 0.020	
Transient, staging (N/Y)[§*]	M	staging & transient	individual (n = 629)	0.084 ± 0.013	0.041 – 0.089	<0.0001
			year, ring age, wintering area	0.019 ± 0.006	0.011 – 0.036	
Date of arrival[§]	M	staging & transient	individual (n = 629)	0.163 ± 0.027	0.109 – 0.217	<0.0001
			year, ring age, wintering area	0.055 ± 0.012	0.035 – 0.082	
	M	staging	individual (n = 488)	0.157 ± 0.043	0.077 – 0.243	<0.0001
			year, ring age, wintering area	0.067 ± 0.016	0.042 – 0.104	
	M	transient[#]	individual (n = 439)	0.136 ± 0.057	0.016 – 0.251	0.01
			year, ring age, wintering area	0.025 ± 0.012	0.009 – 0.057	
	F	transient[#]	individual (n = 25)	0.235 ± 0.161	0.000 – 0.573	0.1
			year, ring age, wintering area	0.117 ± 0.087	0.025 – 0.349	
Date of departure[§]	M	staging & transient	individual (n = 629)	0.204 ± 0.029	0.144 – 0.259	<0.0001
			year, ring age, wintering area	0.011 ± 0.005	0.004 – 0.025	
	M	staging	individual (n = 488)	0.172 ± 0.045	0.090 – 0.269	<0.0001
			year, ring age, wintering area	0.012 ± 0.008	0.003 – 0.032	
Minimal stopover duration[§]	M	staging & transient	individual (n = 629)	0.224 ± 0.028	0.171 – 0.279	<0.0001
			year, ring age, wintering area	0.035 ± 0.011	0.017 – 0.061	
	M	staging	individual (n = 488)	0.111 ± 0.043	0.030 – 0.200	<0.0001
			year, ring age, wintering area	0.022 ± 0.010	0.009 – 0.048	

R: Repeatability, SE: standard error, CI: confidence interval, N: number of different individuals included. [†]Resighted 2005–2019 (2006–2013 for the other variables). [§]LMM, including the setting 'adjusted=FALSE', which adds the variance explained by the fixed effects (year, ring age, sex, wintering area) to the denominator of the repeatability equation. [#]date of observation of transients: date of arrival and departure on the same day. [*]binomial GLMM, original-scale approximations shown.

Table S10. Comparison of presence and behaviour of male Ruffs marked 10 km north of the study area (Wommels) and in the study area. Individuals were marked in 2004–2012, and resighted in 2005–2019 in the study area. Data for 'behaviour' (type, arrival, departure, minimal stopover duration) are based on resightings from 2006–2013 only. Given are means and SD. *n*: sample size.

Variable	Wommels	Study area	Test
Total marked	451	4756	
Proportion resighted (n)	0.46 (204)	0.43 (2030)	Fisher's exact test: $P = 0.3$
Proportion staging (n)	0.36 (118)	0.48 (1425)	GLMM: $z = -4.6$, $P < 0.0001$
Arrival day – staging	88.9 ± 11.4	86.7 ± 10.9	LMM: $\chi^2_1 = 1.8$, $P = 0.2$
Departure day – staging	107.1 ± 10.8	104.4 ± 10.9	LMM: $\chi^2_1 = 4.1$, $P = 0.04$
Minimal stopover duration	18.2 ± 13.4	17.8 ± 12.1	LMM: $\chi^2_1 = 0.6$, $P = 0.4$
Date of transient visit	97.3 ± 12.1	95.8 ± 12.6	LMM: $\chi^2_1 = 0.02$, $P = 0.9$