Since 1962, with the implementation of the European Common Agricultural Policy which led to agricultural intensification, lowland grassland areas in Europe have changed profoundly, with great negative impact on biodiversity (Vickery et al. 2001, Donald et al. 2001, 2006, Sutherland et al. 2012). In The Netherlands, the wet grasslands that were lost provided an ideal habitat for breeding and staging shorebird populations of international importance (Beintema et al. 1995, BirdLife International 2004). The moist soils enabled good access to soil dwelling invertebrates, and the heterogeneous swards favoured abundant insect life and
provided cover for small chicks (Beintema et al. 1995). The modern agricultural practices for dairy production involve increasing levels of mechanization and the use of agrochemicals, high nitrogen input, soil drainage, high resowing rates, seasonal advances in harvesting dates and increased stocking densities (Bos et al. 2013). Modern meadows no longer provide abundant and available invertebrate prey (Vickery 2013). Modern meadows no longer provide abundant and available invertebrate prey (Vickery et al. 2001). In The Netherlands as a whole, only a few percent of the original biodiverse grasslands are left untouched, most of the rest have been turned into drained monocultures of dense and fast growing ryegrass variants (Lolium sp.) or corn fields (Zea mays; e.g. Groen et al. 2012).

The increasing prevalence of intensively managed grasslands with early mowing regimes has had a clear negative impact on the productivity of breeding shorebirds such as Black-tailed Godwits Limosa limosa, Northern Lapwing Vanellus vanellus and Redshank Tringa totanus (Roodbergen et al. 2012, Schekkerman & Beintema 2007, Kleijn et al. 2010, Kentie et al. 2013). The resulting decline raised concerns and eventually the wish to counteract the losses led to agro-environmental schemes (Kleijn et al. 2001, Verhulst et al. 2007), mosaic management (Schekkerman et al. 2008) and other local initiatives (van Paassen & Roetemeijer 2006), although with mixed and perhaps rather limited success (Kleijn et al. 2001, Verhulst et al. 2007). Much less attention has been given to the use of the same agricultural fields by large passage populations of shorebird species including Lapwing Vanellus vanellus, Eurasian Golden Plover Pluvialis apricaria and Ruff Philomachus pugnax (Hornman et al. 2013). Yet, the quality of staging areas is as crucial to the fate of populations as is the quality of breeding areas (Piersma & Baker 2000, Piersma et al. 2016); adequate staging enables migrants to timely and safely replenish energy stores in order to successfully complete migrations (e.g. Alerstam & Lindström 1990, Alves et al. 2012).

Here we document changes in the use of agricultural fields with different characteristics by spring-staging Ruffs over a period of decline. In early March, flying from their winter quarters in the floodplains of sub-Saharan Africa, Ruffs land in the agricultural areas of southwest Friesland to replenish their energy stores before continuing their migration towards breeding grounds in northern Eurasia (van Rhijn 1991, Cramp & Simmons 1983, Jukema et al. 2001b). This lekking sandpiper is well known for the spectacular plumage colour polymorphism of males (van Rhijn 1991, Widemo 1998, Jukema & Piersma 2006, Küpper et al. 2016). Independents and satellites are twice the size of females and develop extravagant nuptial plumages. Faeders, in contrast, keep an inconspicuous plumage resembling females whilst being only slightly larger. Males migrate ahead of females to form leks on breeding grounds and none of them take part in parental care (van Rhijn 1991, Verkuil et al. 2008). The striking differences between the sexes imply that during most of the annual cycle males and females live apart, each according to their own ecological needs (van Rhijn 1991).

In the late 1990s, the spring passage population of Ruffs in The Netherlands went into steep decline. Peak numbers of the Frisian night roosts fell from over 25,000 birds in the 1990s to 3000–5000 in the 2000s (Verkuil et al. 2012, Schmaltz et al. 2015), although apparently stabilizing since (Hornman et al. 2013). This decline is part of a larger population decrease of western Ruffs since the late 20th century (Rakhimberdiev et al. 2011), a change that has been suggested to reflect the loss of good staging habitats along the flyway (Verkuil et al. 2012), but also increased hunting pressures in the Sahel region (Zwarts et al. 2009), and even climate warming at breeding latitudes (Zöckler 2002, Virkkala & Rajasärkkä 2011). With reference to our study population, recent studies have suggested that staging Ruffs may be challenged (i.e. show declines in population wide daily body mass increment) by the quality of the grassland staging habitats in southwest Friesland (Verkuil et al. 2012). A transect survey conducted in 2003, examining sex differences in meadow use, showed that Ruffs generally preferred the most open meadows with short vegetation close to roosting sites. Yet, females were more strongly associated with wet edges and the less drained meadows than males (Verkuil & de Goeij 2003).

Here we report on the foraging distribution of Ruffs during eight successive spring staging seasons (2006–2013) based on daytime resighting locations of individually colour-ringed birds. Moreover, in 2013 we repeated the transect survey on foraging Ruffs conducted in 2003 (Verkuil & de Goeij 2003). We will interpret the presence, especially of male Ruffs, with reference to data on agricultural intensity, soil type and distance to the nearest roosting site, and will discuss our results considering the distinct use of wet edges by females. This work aims to improve our understanding of the behaviour of Ruffs staging in a modern agricultural landscape and contribute to identifying relevant habitat conservation measures.
METHODS

Study area and study system
Field work was carried out in southwest Friesland in an area bordered by the villages of Makkum (53°3.37’N, 05°24.19’E) in the north and Laaksum (52°51.15’N, 05°24.77’E) in the south, by the shores of Lake IJsselmeer in the west, and by the village of It Heidenskip (52°56.93’N, 05°30.11’E) in the east (Groen et al. 2012). The study area of 9855 ha encompasses 50 polders (or water management areas, see Figure 1A), and is representative of the modern Dutch agricultural landscape. Intensively managed land largely predominates (80%) including monocultures of ryegrass and arable land. The remaining 20% consists of traditionally extensively managed fields (herb-rich meadows) mostly maintained as meadowbird reserves (Groen et al. 2012; Figure 1B). Since 2010, thanks to local initiatives, several inland wetlands have been created for shorebirds, by either flooding meadows, opening small waterbodies and/or clearing and reshaping shallow edges of established wetlands (pers. obs.).

In spring, migrating Ruffs stage in southwest Friesland from mid-March to mid-May. Males arrive first and are much more numerous than the females which only appear in mid-April (Wymenga 1999, Verkuil & de Goeij 2003, Schmaltz et al. 2015). Staging Ruffs show a strong daily rhythm, in which the daytime foraging is stopped to enter a period of rest broadly between 12:00 and 15:00, henceforward termed ‘midday siesta’ (Piersma 1983, Verkuil & de Goeij 2003). Ruffs then gather mostly in the inland wetlands of the study area, but can also be observed at the roosting sites along the shores of Lake IJsselmeer (Figure 1A).

![Figure 1](https://example.com/figure1.png)

**Figure 1.** (A) Map of the study area, with polder units, and roosting sites. For the colour-ring resighting study, the polder units are separated by dark red lines for 2006–2008, with additional distinctions in the period 2009–2013 indicated with dashed dark red lines. The meadows of the transect survey are represented in bright green colour. Newly created inland wetland sites used as daytime roost (from 2009 onwards) are illustrated with striped circles and established wetland sites (used before 2003) with empty circles. The night-time roosting sites are represented with grey circles. (B) Map of the study area with vegetation typology with herb-rich grasslands represented in orange, herb-poor meadows in green, and unscored vegetation is indicated in grey.
Colour-ring resightings and mapping
To quantify changes in the distribution of staging Ruffs, we used resighting data from colour-marked Ruffs captured in the study area as part of a demographic programme initiated in 2004 (Verkuil et al. 2010, Schmaltz et al. 2015). From 2006–2013, the catching and resighting efforts were rather constant in space and time: 15 to 20 catchers (the ‘wilsternetters’) were similarly active over the entire study area every year. Ruffs were captured using a traditional method with a large 20 by 3 m, wind-assisted, clap net (Jukema et al. 2001a, Piersma et al. 2005). Captured Ruffs were marked individually with an unique combination of four PVC colour-rings and one colour-flag attached on both tibiae and/or tarsi (Verkuil et al. 2010). Each individual was also measured, sexed and weighed.

Each spring, resightings were obtained by 4 to 5 observers using telescopes (20–60×65 and 20–60×80). The entire study area was surveyed by driving or biking along country roads from the morning until the evening, whilst inspecting the roosts during midday. The observation effort of up to 10 h per day was maintained six days a week. The whole area was covered roughly every two days. The flat, open landscape and the dense road network allowed most flocks to be approached with relative ease. Thus, our observation effort assured near-complete coverage of the study area.

Prior to 2009 observations of individual colour-ringed Ruffs were recorded within large polder units (i.e. set of meadows). From 2009 onwards, each meadow of the study area was referenced and grouped within smaller polder units. Hence, from 2009 to 2013 each observation has been assigned within small polder units. Accordingly, the number of colour-ring resightings were mapped using ArcGIS 10.1 software, by ‘large’ polder units in 2006–2008 and by ‘small’ polder units after 2009 (Figure 1A).

Transect survey
In 2013 we repeated the transect survey carried out in 2003 (Verkuil & de Goeij 2003). Similar to 2003, the fields along surveys covered 656 ha spread over six polders (Figure 1A). Some fields had been split since 2003, and this added 10 meadows to the 125 meadows surveyed ten years earlier. Two observers visited every meadow (n = 135) once a week between 10:00 and 12:00 and recorded the presence or absence of Ruffs. When birds were detected, we also recorded whether males and/or females were present in the group. However, the lack of females present currently on the study site (Schmaltz et al. 2015) did not allow us to consider the distribution of the sexes independently. The survey was performed during five weeks, from the first week of April to the first week of May, when most Ruffs are present.

Using the transect surveys data of 2013, we looked at correlates of Ruff presence with farming and landscape characteristics at the meadow level. We assumed that staging Ruffs select meadows allowing high intake rates (Piersma 2012, J. Onrust et al. in prep.) and we hence considered agricultural intensity, a factor that might directly affect the availability of invertebrate prey. We expect Ruffs to use the least intensively managed fields, as soil drainage combined with high and dense swards are thought to reduce prey availability (McCracken & Tallowin 2004). Herb-richness was used as a proxy for level of agricultural intensity (Groen et al. 2012). Data on herb-richness at the meadow level was adapted from the characterization made in 2009 by Groen et al. (2012), so that the herbpoor level corresponded to intensively managed meadows and the herb-rich to the extensively managed meadows (Figure 1B).

We also considered three soil types present in our study area (clay, peat and sand) as correlates. Peat soil that maintains a greater upper soil moisture than clay and sandy soil should enhance food availability and field attractiveness for staging Ruffs (Edwards & Bohlen 1996). For soil type we used the 2003 data. Next, we expect that staging Ruffs will feed close to resting areas to minimize the energy expended on commuting flights (Rogers et al. 2006, Dias et al. 2006, van Gils et al. 2006). For each meadow, we characterized the distance to roosting areas as the distance (in m) between the centre of a meadow and the nearest roost. Those included the night-time roosting sites on the shoreline of Lake IJsselmeer and all inland wetlands. The distance calculations were made with ArcGIS 10.1 software. We performed the statistical analysis on a complete case dataset (n = 104 fields), ignoring meadows for which herb-richness and soil type were not recorded (see Figure 1). We do not expect this to have any impact on our biological inference as these meadows in all aspects were comparable to the others.

We used Generalized Linear Mixed-effects models to investigate the effects of herb richness, soil type and distance to the nearest roost on the occurrence (i.e. presence/absence) of staging Ruffs during the transect survey in 2013, with meadow and week number as random factors. We acknowledge that we modeled here an apparent occurrence probability as we do not account for imperfect detection probability (i.e. during the survey, Ruffs may not always be found in all the
meadows were they actually occur). Model selection was done following an Information Theoretic approach (see Grueber et al. 2011) using package MuMIn (Bartón 2009) in statistical software R, version 3.2.0. (R Core Team 2015). From the global model (model 2, Table 1), eight competing and biologically relevant models were fitted to the data (Table 1). The relative support of competing models was assessed with Akaike Information Criterion corrected for small sample size (AICc – best supported model having the lowest AICc values) and Akaike weight \( w_i \) (Burnham & Anderson 2002). The relative importance of variables, weight averages of parameter estimates and confidence intervals were calculated by averaging models with a \( \Delta \text{AICc} \leq 2 \) (models fitting the data equally well – Burnham & Anderson 2002).

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>( \Delta_i )</th>
<th>( w_i )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil + Distance</td>
<td>228.6</td>
<td>0.00</td>
<td>0.64</td>
</tr>
<tr>
<td>Herb-richness + Soil + Distance</td>
<td>229.8</td>
<td>1.24</td>
<td>0.35</td>
</tr>
<tr>
<td>Herb-richness + Distance</td>
<td>237.7</td>
<td>9.12</td>
<td>0.01</td>
</tr>
<tr>
<td>Soil</td>
<td>238.3</td>
<td>9.73</td>
<td>0.00</td>
</tr>
<tr>
<td>Herb-richness + Soil</td>
<td>239.5</td>
<td>10.87</td>
<td>0.00</td>
</tr>
<tr>
<td>Distance</td>
<td>244.9</td>
<td>16.28</td>
<td>0.00</td>
</tr>
<tr>
<td>Herb-richness</td>
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<td>35.37</td>
<td>0.00</td>
</tr>
<tr>
<td>Null model</td>
<td>267.0</td>
<td>38.41</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Table 1. Results of model selection explaining the occurrence of staging Ruffs during the transect survey of 2013, as function of farming (Herb-richness) and landscape structure variables (Distance to roosting areas and Soil type). Akaike’s information criteria corrected for small sample sizes (AICc), AIC differences \( \Delta_i \) and Akaike weights \( w_i \) are shown for each model and a null model for comparison. Models with equal support \( \Delta_i \leq 2.0 \) are specified in bold.

Staging Ruffs foraging on a wetted meadow at the Ursuladyk in It Heidenskip (foto: Lucie Schmaltz, 6 April 2012).
Figure 2. The numerical distribution of resightings of colour-ringed Ruffs from 2006 to 2013 per polder unit and roosting sites available to the birds (including all inland wetlands and night-time roosts (grey dots)). The map at the bottom right represents the distribution of the resightings at meadow-level in the centre of the area in 2013 in relation to herb-richness and roosts (herb poor indicated in green vs. herb rich fields in orange, unscored in grey; new inland wetlands represented with striped circles, established inland wetlands with empty circles and night-time roosts with grey circles). Numbers of sightings are represented using a colour intensity scale and a dot-size scale (detail).
RESULTS

The distribution of resightings of marked Ruffs showed considerable change in the course of the years (Figure 2). The most northern and southern parts of the study area were abandoned in the course of time. After inland wetlands were created in 2010 in the central area, numbers of resightings here built up, especially in 2012 and 2013.

Ruffs occurred at least once in only 30 meadows out of the 135 of the transect, suggesting a rather low occupancy rate of the study site, which is in line with the small number of migrants staging in Friesland in 2013. Model selection showed that two models fitted our transect data equally well (models 1 and 2, ΔAICc ≤ 2; Table 1). Model 1, that considered soil type and distance to a roosting area, received the best support. Model 2 was slightly less well supported than model 1 (ΔAICc = 1.24), thus adding herb-richness to explain Ruff occurrence did not improve the fit to our data.

Models that did not consider soil type and distance to a roost performed poorly (ΔAICc with model 1 ≥ 9.12). The final model-averaged parameter estimates (based on model 1 and 2) revealed that the probability of occurrence of staging Ruffs was positively associated with sandy soil and short distances to roosting areas (confidence intervals do not overlap with 0; Table 2, Figures 3A and 3B).

DISCUSSION

On the basis of the resighting maps, between 2006 and 2013 staging Ruffs progressively concentrated in the central part of the study area (Figures 1 and 2). That this occurred after 2010 is especially interesting, because it coincided with the creation of new small inland wetlands and the restoration of existing ones where Ruffs could congregate for their 'siestas' during the middle of the day. The transect survey confirms this
pattern and also showed that the likelihood of encountering Ruffs was higher in fields closer to a roost (Figure 3A). This is consistent with what Verkuil & de Goeij (2003) found a decade earlier.

Ten years apart, both surveys showed that ruffs primarily forage near resting areas. This fits our expectation that staging Ruffs would limit movements between feeding and resting areas and thereby reduce flight costs. However, these inland wetlands may also constitute good feeding areas, especially for females, as the presence of standing shallow water may provide an alternative source of aquatic invertebrates (e.g. Chironomids, see Sanders 2000). Indeed, female Ruffs obtain their prey by pecking rather than by probing in the soil, so that larvae and emerging adults of aquatic insects might constitute an important part of their diet (Verkuil & de Goeij 2003).

The preference for sandy soil (Figure 3B) goes against our prediction that Ruff will prefer peat, which would more easily maintain a moist upper layer. However, that Ruffs were more likely to be encountered on sandy soils may simply reflect a preference for the Workumervaard polder, situated in the centre-north of the study area (see Figure 1A). The Workumervaard has sandy soils but otherwise shows all key habitat features attractive for Ruffs (herb-rich and open vegetation, a short sward maintained by the grazing of 1000s of Barnacle Geese Branta leucopsis during the entire passage period of Ruffs (Kleijn & Bos 2010), relatively high water tables, open landscape, proximity to roosts). A posteriori, we looked at the probability of occurrence of Ruffs among polders occupied at least once and suggested that the likelihood to encounter Ruffs was indeed the highest on the Workumervaard (Figure 3C). In parallel, most resightings were made on this polder (see Figure 2).

Arguably the most interesting pattern is that numbers of staging Ruffs did not decline evenly across the study area. Instead, Ruffs tended to clump in the centre of the study area where most inland wetlands were found thanks to the local initiatives that created new ones, but also keep improving already established wetlands. There was no trend towards warmer and drier springs in the end of the study period to explain why the remaining spring staging Ruffs retreated to the wet areas.

Yet, a long-standing question has been the function of the siesta for Ruffs, during which they preen and sleep. Here, and increasingly so in the course of the spring season, Ruffs also initiate lek-type displays including male-male fights. We suggest that a possible reason for the concentration of Ruffs around inland wetland sites is the possibiltiy to engage with females, triggering sexual activity and female-following even at a time when the birds have not yet reached their full sexual maturity (Jukema & Piersma 2006).

Our study indicates that inland wetland sites used as feeding and roosting sites provide important, and possibly critical, habitat for Ruffs staging in southwest Friesland. Long-term monitoring efforts of meadow bird populations in relation to land use, such as presented here, are as rare as they are necessary for assessments of the quality of the habitats for birds. We suggest that the creation of new wet grassland areas and small waterbodies in the province of Friesland will indeed have helped create suitable foraging habitat for females, with cascading positive effects on the attractiveness of these wetlands (and the surrounding meadows) for males. Within a modern agricultural landscape, the importance of Workumervaard illustrates that the maintenance of traditionally managed polderland, holding high quality foraging land and resting areas, is critical to keep these spectacular passage migrants in the Frisian landscape.

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SAMENVATTING

De intensieve melkveehouderij heeft de graslanden in de agrarische gebieden van Nederland grondig veranderd, met negatieve effecten op de voortplanting van de steltlopers die er broeden. Dit moderne agrarische landschap wordt ook gebruikt door steltlopers om te ruiken en op te vetten tijdens de trek, maar de functie als doortrekgebied krijgt veel minder aandacht dan de functie als broedgebied. Gedurende een periode van tien jaar hebben wij in het voorjaar de Kemphanen Philomachus pugnax bestudeerd die op weg naar het noorden en in de graslanden van Zuidwest-Friesland pleisteren. In de onderzoeksperiode namen de piekaantallen af van 20.000 vogels in 2003 tot 3500 in 2009, waarna de aantallen stabiliseerden. Gebruikmakend van de plaatsen waar met kleurringen gemerkte individuen verbleven, beschrijven wij de veranderingen die tussen 2006 en 2013 in de ruimtelijke verspreiding van overdag foeragerende Kemphanen zijn opgetreden (‘s nachts verblijven de vogels op gemeenschappelijke slaapplaatsen). In de loop van de jaren trokken de Kemphanen zich meer en meer terug in het midden van ons studiegebied van 10.000 ha. Daar werden, tussen de intensief beheerde weilanden, bestaande en recent ontwikkelde natte gebieden gebruikt om te foerageren of te roezen. Om mogelijke veranderingen in het ruimtelijk gebruik van het gebied te kwantificeren, hebben wij in 2013 een transect-inventarisatie uit 2003 herhaald. Door kruisrondjekom (als maat voor intensiteit van agrarisch gebruik) en landschapskenmerken (afstand tot de slaapplaats, grondsoort) op een vergelijkbare manier te karakteriseren, konden we aantonen dat in het voorjaar van 2013, net als in 2003, Kemphanen het liefst zo dicht mogelijk bij een slaapplaats foerageren. De inventarisaties brachten ook aan het licht dat Kemphanen een voorkeur hebben voor de Workumwaard, een bijzonder grote, open en grotendeels extensief beheerde polder met een zanderige bodem en een korte vegetatie, grenzend aan een traditionele slaapplaats direct aan de kust. Ons onderzoek levert indirect bewijs voor de stelling dat de aanleg van natte gebieden of plas-dras situaties binnen een gebied dat gedomineerd wordt door moderne graslanden, het gebied aantrekkelijker zal maken voor doortrekkende Kemphanen.

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