

RESEARCH ARTICLE

Earthworm abundance and availability does not influence the reproductive decisions of black-tailed godwits in an agricultural grassland

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Abstract

1. Maintaining the biodiversity of agricultural ecosystems has become a global imperative. Across Europe, species that occupy agricultural grasslands, such as black-tailed godwits (*Limosa limosa limosa*), have undergone steep population declines. In this context, there is a significant need to both determine the root causes of these declines and identify actions that will promote biodiversity while supporting the livelihoods of farmers.
2. Food availability, and specifically earthworm abundance (Lumbricidae), during the pre-breeding period has often been suggested as a potential driver of godwit population declines. Previous studies have recommended increasing the application of nitrogen to agricultural grasslands to enhance earthworm populations and aid agricultural production. Here we test whether food availability during the pre-breeding period affects when and where godwits breed.
3. Using large-scale surveys of food availability, a long-term mark-recapture study, focal observations of foraging female godwits, and tracking devices that monitored godwit movements, we found little evidence of a relationship between earthworm abundance and the timing of godwit reproductive efforts or the density of breeding godwits. Furthermore, we found that the soils of intensively managed agricultural grasslands may frequently be too dry for godwits to forage for those earthworms that are present.
4. The increased application of nitrogen to agricultural grasslands will therefore likely have no positive effect on godwit populations. Instead, management efforts should focus on increasing the botanical diversity of agricultural grasslands, facilitating conditions that prevent hardening soils, and reducing the populations of generalist predators.

KEYWORDS

agricultural biodiversity, *Limosa limosa*, Lumbricidae, nitrogen, phenological mismatch

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1 | INTRODUCTION

Maintaining the biodiversity of agricultural ecosystems has become a global imperative as more land is converted to agriculture and as agricultural lands are farmed with increasing chemical and energy inputs (Tschamntke et al., 2012). The European Union provides a stark example: despite billions of euros spent annually on agricultural subsidies with the goal of maintaining biodiversity, populations of plants, insects and birds are rapidly declining on agricultural lands across the region (Habel et al., 2019; Krauss et al., 2010; Storkey et al., 2012). In this context, there is a tremendous need to both determine the root causes of these declines and identify actions that will promote biodiversity while supporting the livelihoods of farmers (Garibaldi et al., 2017).

Among the species declining most rapidly in European agricultural ecosystems are the 'meadowbirds' that breed in agricultural grasslands (Thorup, 2006). In particular, the nominate subspecies of the black-tailed godwit (*Limosa limosa limosa*; hereafter 'godwit') – of which more than 90% breed in agricultural grasslands within the European Union – has experienced a dramatic decline (Gill et al., 2007). Following population declines of more than 75% over the past four decades, godwits have been labelled near threatened by the IUCN and made the focus of considerable conservation and management efforts (Kentie et al., 2016). Despite this attention, recent years have witnessed accelerated declines and record-low indices of reproductive success across the godwit range (Loonstra et al., 2019; Verhoeven, Smart et al., 2021).

The proximate causes of the godwit population decline – and of the declines of meadowbirds more generally – include direct nest loss to agricultural practices (Kruk et al., 1996), increased nest predation rates (Kentie et al., 2015; Verhoeven, Smart et al., 2021) and low growth rates and survival among juveniles (Kentie et al., 2013; Loonstra et al., 2018, 2019; Schekkerman & Beintema, 2007). Two broad-scale factors are thought to underlie these proximate causes: (1) the mismatch that has developed between the timing of godwit reproductive efforts and the phenology of their grassland habitats (Kleijn et al., 2010; Schroeder et al., 2012) and (2) that large numbers of godwits persist in breeding in low-quality habitats (Groen et al., 2012; Kentie et al., 2014). The phenological mismatch results in godwits nesting late relative to the period of growth of agricultural grass species; as a result, godwits are still incubating their nests when farmers mow the fields, and the nests are thereby vulnerable to both mowing-related losses and the efforts of generalist predators (Kentie et al., 2015; Kruk et al., 1997). For those nests that do hatch, the mismatch subsequently results in chicks missing the peak of invertebrate availability and encountering a relatively resource-poor environment (Loonstra et al., 2018; Schekkerman et al., 2009). The effects of the mismatch on godwit population dynamics are then compounded by the fact that a large proportion of the population continues to breed in high-intensity agricultural grasslands where nest predation rates are particularly high and chick survival rates especially low (Kentie et al., 2013; Kruk et al., 1997; Loonstra et al., 2019). Godwits are thus expected to have higher reproductive success when breeding earlier and in less intensively managed grasslands (Kentie et al., 2018).

The availability of the primary prey of adult godwits – earthworms (Lumbricidae; Beintema et al., 1995) – is thought to underlie godwit decisions about when and where to breed, and therefore contribute to both their current phenological mismatch and their persistence in breeding in low-quality habitats (Musters et al., 2010). Some studies, for instance, have suggested that earthworms may be present in insufficient numbers during the godwit pre-breeding period as the birds allocate resources to their eggs (Brandsma, 1999; Musters et al., 2010). If true, this could explain why female godwits often spend up to 5 weeks on the breeding grounds prior to initiating their clutches (Lourenço et al., 2011; Senner et al., 2015). Additionally, low-intensity agricultural grasslands have historically been thought to provide fewer food resources for adult godwits than high-intensity ones (Brandsma, 1999; Hut & Helmig, 2003; Siepel et al., 1990). Discussions of management efforts that might both narrow the phenological mismatch for godwits and encourage them to nest in less intensively managed grasslands have therefore largely focused on food availability during the pre-breeding period (Kleijn et al., 2010; Musters et al., 2010).

Among the differences between low- and high-intensity agricultural grasslands is the nitrogen level of the soils in the two habitats (Groen et al., 2012). While high nitrogen inputs have pronounced negative effects on botanical diversity and above-ground invertebrates (Kleijn et al., 2008; Nessel et al., 2021), these inputs are thought to both promote the rapid growth of agricultural grass species and improve earthworm abundance (Brockman, 1969; Edwards & Lofty, 1982). The increased allocation of nitrogen in order to promote earthworm abundance has therefore often been recommended as a practice to boost godwit populations in agricultural grasslands across management intensities (Brandsma, 1999; Kleijn et al., 2009a; van der Weijden & Guldmond, 2006). More recently, however, the nitrogen-earthworm-godwit paradigm has been called into question. Soil type may actually have more to do with earthworm abundance than nitrogen levels (Onrust, Hobma et al., 2019), while topsoil desiccation may lower earthworm availability for meadowbirds in high-intensity agricultural grasslands (Nordström, 1975; Onrust, Wymenga et al., 2019). Further investigations of the role that earthworm abundance may play in either constraining or facilitating godwit reproductive efforts are therefore needed.

Our study investigates the relationship between earthworm availability and godwit reproductive efforts in southwest Friesland, The Netherlands. Using a multi-year dataset comprised of large-scale surveys of earthworm abundance, intensive focal observations of marked female godwits, and data from miniaturized tracking devices, we tested whether the abundance and availability of earthworms were correlated with the timing of arrival, duration of the pre-breeding period, egg size, and selection of breeding territories in godwits. We predicted that earthworms would be less abundant during the pre-breeding period than during the nest incubation period, and that godwits would arrive earlier, nest earlier, and nest in higher densities in areas with higher earthworm abundances (Brandsma, 1999; Högstedt, 1974). The outcome of our study will directly contribute to the development of sound management directives that can help halt the decline of this species of high conservation concern.

TABLE 1 The main differences between the two types of grassland management in our study area; see Groen et al. (2012) for a more in-depth description of these two management types

	High-intensity grasslands	Low-intensity grasslands
Spring groundwater level	± 90 cm below surface	± 20 cm below surface
Type of nitrogen application	Slurry + artificial fertilizer	Farmyard manure
Amount of manure	± 70 tons/ha	0–25 tons/ha
Nitrogen level	± 300 kg/ha	0–100 kg/ha
Mowing frequency	4–7 times/year	1 time/year
Number of cattle grazed	No grazing	0–5 cows/ha
Botanical diversity ^a	1–3 plant species	> 10 plant species

^aFrom Groen et al. (2012).

2 | MATERIALS AND METHODS

2.1 | Study area

We studied the relationship between the reproductive decisions of godwits and earthworm abundance in the Haanmeer (52.9222°, 5.4353°), a 200-ha polder in southwest Friesland, The Netherlands. The Haanmeer polder is one of the last remaining areas with high densities of breeding godwits (~0.5 pairs/ha) in southwest Friesland – which represents the core of the godwit breeding distribution (Kentie et al., 2016) – and is part of a long-term landscape-scale study of godwit demography and breeding biology (see Groen et al., 2012; Senner et al., 2015 for more details). The Haanmeer consists of fields that are maintained under two different management schemes: (1) high-intensity grasslands (70 ha) and (2) low-intensity grasslands (130 ha). The two management types differ in a number of ways, including water levels, botanical richness, the number of cattle grazed, amount and type of nitrogen application, and mowing regime (Table 1).

In particular, the application of cow manure – the main source of nitrogen input – averages ~70 tons/ha on the high-intensity grasslands, but only ranges from 0 to 25 tons/ha on the low-intensity grasslands (A. Stokman, S. Venema and D. Postma, personal communication, 2013). In addition, the water level in the ditches surrounding the fields is kept consistently lower in the high-intensity grasslands (unpublished data, Wetterskip Fryslân) resulting in a ~70-cm difference in spring groundwater level (unpublished data, MAV and NRS). These two management types and the differences between them are typical for our study area (see Groen et al., 2012) and the godwit breeding range in the Netherlands (Teunissen et al., 2012).

2.2 | Data collection on godwit behaviour

In the period 2008–2012, we captured 87 adult and 392 juvenile godwits in the Haanmeer and surrounding polders. Upon capture, adults and chicks were individually marked, bled for molecular sexing, and measured for biometrics (see Loonstra et al., 2019). The latter included the measurement of their exposed culmen to the nearest millimetre (hereafter 'bill length'). The individual markings consisted of a unique

colour-ring combination for adults and appropriately sized chicks and a single flag with a unique alphanumeric code for smaller chicks.

In 2013 and 2014, we searched daily for these individually marked godwits as they returned to the Haanmeer. We started with the first arrival of adults and continued until the first egg was found (2013: 8 March–10 April; 2014: 8 March–9 April). When an individually marked godwit was encountered, its colour code, location, and behaviour – foraging, preening, displaying, etc. – were recorded. During the same period, we made daily foraging observations on a subset of individually marked females. For these females, we recorded the number of probes and successes during consecutive 3-min periods, where a probe was defined as a downward movement of the bill into the soil and success as a swallowing motion (Senner & Coddington, 2011). When possible, we also recorded the prey type consumed. In 2013, we observed a foraging individual for up to ten 3-min periods for a total daily foraging observation length of 30 min. In 2014, we did this for up to three 3-min periods for a total daily foraging observation length of 9 min.

In 2014, we also tracked the locations of three females throughout their pre-breeding period using 7.5 g solar-powered UvA-Bits GPS trackers (Bouten et al., 2013). Under license numbers 6350A and 6350C following the Dutch Animal Welfare Act, we attached these trackers in 2013 with a leg-loop harness using 2 mm nylon rope (see Senner, Stager, Verhoeven et al., 2018 for more details). These trackers stored location estimates once every 5 min when the battery was fully charged and once every 15–30 min in all other instances. One of these females was still carrying its transmitter in 2015, and this provided us with an additional year of spatial distribution data during the pre-breeding period.

After the first egg was found, we stopped our foraging observations and started intensively searching for godwit nests. We floated and measured the dimensions of eggs to estimate incubation stage and egg volume (Liebezeit et al., 2007; Schroeder et al., 2009). We monitored nests every 2–3 days to determine their precise hatching date. We made a particular effort to associate individually marked birds with nests. For nests found in the laying phase, we determined their lay date based on the assumption that godwits lay one egg per day (Cramp & Simmons, 1983). For nests that hatched but were not found in the laying phase, we back-calculated the lay date by subtracting 26 days (the combined average laying and incubation period; Verhoeven et al.,

TABLE 2 Overview of invertebrate sampling in 2013 and 2014

	March 2013	May 2013	March 2014	May 2014
Number of samples	130	136	135	136
Number of samples without worms	23	13	6	8
Number of worms found	1338	890	2331	1746
Mean mass of worm \pm SD	0.197 g \pm 0.199	0.248 g \pm 0.216	0.219 g \pm 0.230	0.212 g \pm 0.242
Percentage of found prey mass that was worm	97.2	89.4	90.1	89.9
Percentage of found prey mass that was <i>Tipula</i> sp. larvae	1.8	10.1	9.4	9.1
Percentage of worms in the top 10 cm	76.7	78.1	85.9	88.4
Predicted worm biomass in the top 10 cm ^a	39.74 g/m ²	31.38 g/m ²	77.71 g/m ²	61.36 g/m ²

^aPredicted from the binomial-gamma hurdle model (see Methods).

2020). In cases where we found a nest with a complete clutch, but did not know the hatching date due to predation or abandonment, we estimated the lay date by subtracting the incubation stage (as derived from the flotation method) from the date the nest was found.

2.3 | Data collection on food availability

On four separate occasions, we sampled the entire Haanmeer for below-ground invertebrates along a 100 \times 150 m grid (Figure 1) as local soil invertebrate populations can vary considerably (Timmerman et al., 2006). In 2013, we collected 130 samples from 1 to 3 March – before the arrival of the first godwits – and 136 samples from 4 to 6 May, just after the last of our individually marked females had begun incubation. We sampled six additional fields in May that had not been sampled in March. In 2014, we collected 135 samples from 8 to 10 March and 136 samples from 1 to 4 May. We inadvertently skipped one sample at the end of a transect in March 2014.

We collected invertebrates in 20 \times 20 \times 20 cm soil samples. To estimate the depth at which invertebrates were present, we split each sample into four pieces along its horizontal axis immediately after removal from the ground, resulting in four equally sized slices 5 cm in height. Each slice was sealed separately in a plastic bag and stored between -5°C and $+5^{\circ}\text{C}$. We processed the samples within 2 weeks by hand-sorting each slice, which is considered the most reliable method (Edwards & Lofty, 1977; Nordström & Rundgren, 1972). We then cleaned all invertebrates, weighed them to the nearest 0.01 g and measured their (relaxed) length to the nearest 0.01 cm.

Soil penetrability affects earthworm availability for godwits by influencing the ease with which godwits can probe the soil for invertebrates (Kleijn et al., 2011). We therefore also measured the penetration resistance of the soil in the same fields in which we sampled soil invertebrates, using a penetrometer with a 1 cm² cone (Eijkelkamp, Giesbeek, penetrometer 06.01.14). From late March to mid-May in 2013, we measured the penetration resistance along four 60 m long transects daily. Two transects each were located in high-intensity and low-intensity grasslands. We sampled every 4 m along each transect, resulting in 15 measurements per transect. To ensure that the results from

our original two transects adequately captured variation in penetrability across the study area, we added eight additional transects in low-intensity grasslands in 2014 for a total of 10 transects in low-intensity grasslands and two in high-intensity grasslands. For these transects, we started in the middle of March and sampled every 2 m along 10 m long transects (six measurements per transect).

2.4 | Statistical analysis of annual and seasonal differences in invertebrate biomass

The recorded invertebrate biomass was zero inflated due to the number of samples without earthworms (Table 2) and included only positive values in those cases when invertebrates were recorded. As a result, we used a two-part binomial-gamma hurdle model. The initial binomial model predicted the probability of recording earthworms in a sample, using a generalized linear mixed model (GLMM) with binomial error structure and a logit link function. The gamma model then predicted the invertebrate biomass when invertebrates were recorded using a GLMM with a gamma error structure and log link function. Both models had year, month, and grassland management intensity as categorical predictor variables, and sampling location as a random intercept to account for pseudo-replication. We obtained chi-squared values for the significance of the predictor variables from likelihood ratio tests of nested models with and without the variable of interest. In the final model, we removed grassland management intensity as a predictor variable because it did not significantly improve the fit in either the binomial or gamma model (see Section 3). By multiplying the predictions of the two parts of the hurdle model (i.e., weighting predicted biomass by the probability of observing an invertebrate), we obtained predictions of invertebrate biomass at both sampling time points in each year.

To additionally test for potentially confounding variables that might influence underlying worm abundances and, therefore, godwit breeding biology, we also ran the same binomial and gamma models with soil type – (1) more clay, (2) more sand, or (3) more peat (Figure 1) – replacing grassland management intensity as a categorical predictor. We excluded three earthworm samples for this analysis, either because

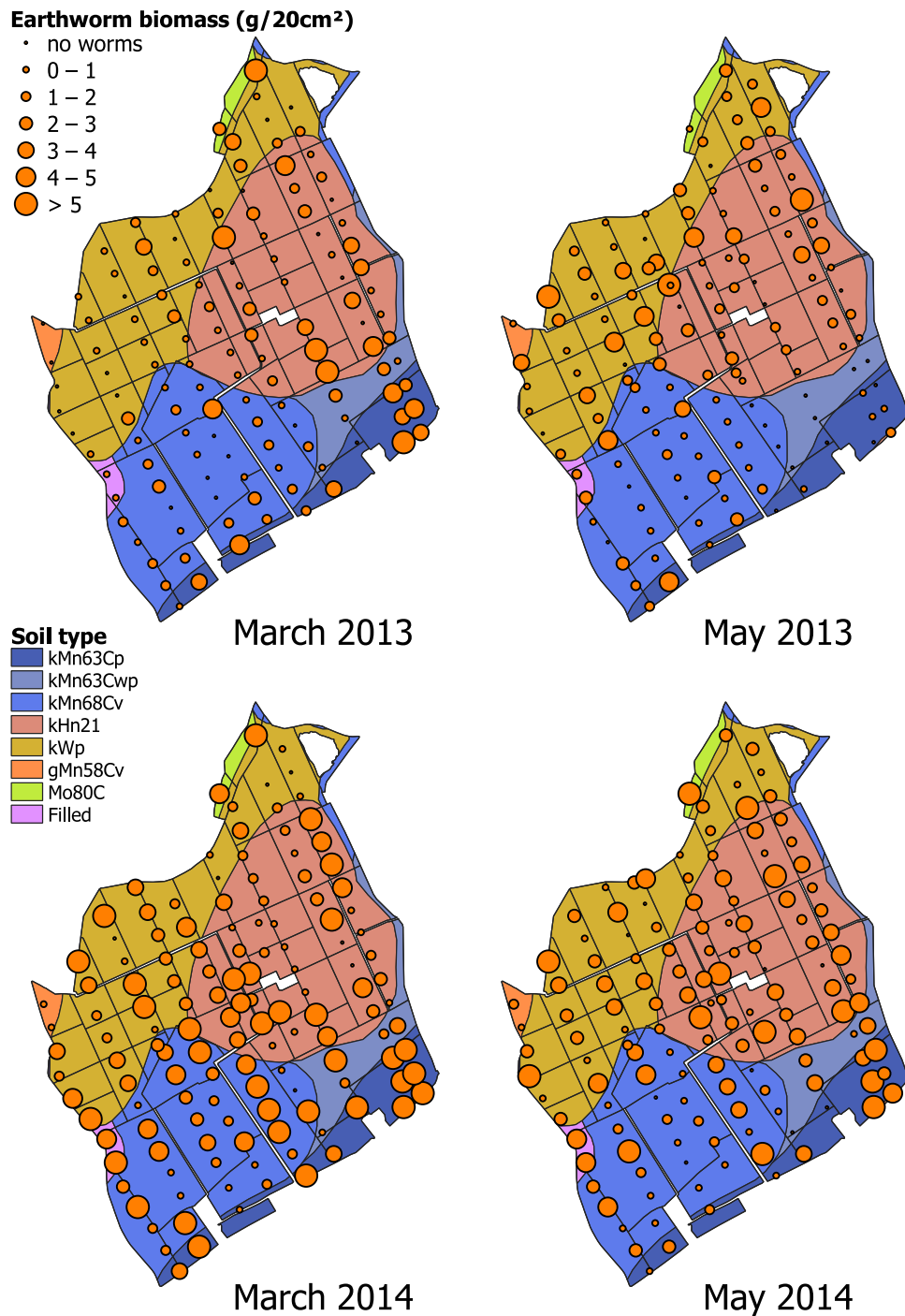


FIGURE 1 Earthworm abundance in the top 10 cm of soil in March and May 2013–2014. Also shown are the soil types in the Haanmeer as recorded in the national database (WUR-Alterra, 2006). Briefly, the blue colours represent soils comprised of more clay, red more sand, yellow more peat, and green more loam. The area in purple was filled with an unknown soil type that had been added from outside the study area. The white areas in the south and middle of the study area are farm buildings, whereas the white area in the northeast corner is a pond

the sampling area had previously been filled with an unknown soil type ($n = 2$) or because the sample was the sole representative of a soil type category (more loam; $n = 1$; Figure 1). Soil type, however, was not a relevant predictor variable of worm abundance in either the binomial ($\chi^2 = 3.07$, $df = 2$, $p = 0.215$) or gamma models ($\chi^2 = 1.76$, $df = 2$, $p = 0.414$), and thus was not included in our final models (Table S1 in the Supporting Information).

2.5 | Relating godwit behaviour to earthworm biomass

Because grassland management intensity and soil type were not related to earthworm biomass (see Section 3), and because prevailing management directives (Brandsma, 1999; Kleijn et al., 2009a; van der Weijden & Guldemond, 2006) posit a direct link between

earthworm abundance and godwit behaviour and abundance – proposing that earthworms explain the observed variation in godwit reproductive phenology and habitat selection – we focused our analyses on testing the relationship between earthworm biomass and godwit behaviour and abundance.

To test for an effect of earthworm abundance on godwit foraging rates, we considered only earthworms in our analyses because earthworms comprised ~90% of prey mass found in March (see Section 3). Furthermore, we used only the earthworm abundance in the top 10 cm because earthworms found deeper in the soil are not within reach of female godwits (see Section 3). We plotted the prey intake rate of female godwits during the pre-breeding periods of 2013 and 2014 against the average earthworm density in the top 10 cm in March of the meadow in which each godwit was foraging. We used only females that probed more than 220 times (25th percentile) and less than 370 times (75th percentile) to control for differences in motivation between individuals, as this is known to cause differences in observed intake rates (Duijns et al., 2015). We then used a Holling type II functional response equation to explore the relationship between intake rate and earthworm density (Holling, 1959). We had no empirical data for handling time (T_h) or instantaneous area of discovery (a) and used the least squares method to calculate the values for both these parameters that yielded the best fit to our data.

We next tested whether earthworm abundance had an effect on where godwits foraged during the pre-breeding period. In a generalized linear mixed model with a Poisson error structure and log link function, we related the number of unique individuals seen on a meadow during the pre-breeding period to the average earthworm biomass in the top 10 cm of that meadow in March, while accounting for the size of the meadow (continuous covariate), the year (two-level factor), and the fact that samples from the same meadow are not independent (random intercept). We ran the same model to relate the number of nests found in a meadow to the average earthworm biomass in the top 10 cm of that meadow in March. For the latter analysis, we included only nests laid before 1 May in order to exclude replacement clutches as much as possible (see Verhoeven et al., 2020).

Third, we related earthworm abundance to godwit breeding phenology. We used linear mixed models to relate the (1) arrival dates, (2) lay dates, and (3) duration of the arrival–laying interval of females to the average earthworm biomass in March in the top 10 cm within 200 m of their nests. We did the same, separately, for the biomass within 300 m of their nests. We included year as a two-level factor and individual as a random intercept. We used the earthworm biomass from within these distances because 70% of the foraging locations of the GPS-tagged females were within 200 m and 88% within 300 m (Figure S1a in the Supporting Information), which is similar to the spatial distribution exhibited by the rest of the population (Figure S1b). In these analyses, we again included only nests laid before 1 May and used chi-squared values to assess the significance of each predictor variable.

Finally, we assessed whether earthworms influenced godwit reproductive investment. For this, we used linear models to relate the lay

dates and average egg volume of all complete clutches (i.e. nests containing four eggs and including those of unknown females) laid before 1 May to the average earthworm biomass in the top 10 cm within 200 and 300 m of these nests in March. We calculated egg volume using the formula: $\text{length} \times \text{breadth}^2 \times 0.52$ (Schroeder et al., 2009). Female size and other covariates were not included in these models, as we have previously shown that they have little effect on egg volume (Verhoeven et al., 2019).

Additionally, we tested the robustness of our worm sampling scheme and our choice to average worm measures across samples within 200 and 300 m of a female's nest or within the meadow in which they nested (i.e. within 500 m or less). Using both Moran's I and Mantel tests, we found evidence of positive spatial autocorrelation or 'clustering' of earthworm biomass at these distances in March 2013 (Moran's I for 200 m = 0.27, $p < 0.001$; 300 m = 0.15, $p < 0.001$; 500 m = 0.1, $p < 0.001$) and March 2014 (Moran's I for 200 m = 0.20, $p = 0.004$; 300 m = 0.09, $p = 0.019$; 500 m = 0.05, $p = 0.021$). Our Mantel tests also indicated that sampling locations nearer to each other had more similar worm abundances, that is positive spatial autocorrelation ($r_{\text{March2013}} = 0.13$, $p < 0.001$; $r_{\text{March2014}} = 0.11$, $p < 0.001$).

We obtained F -values for the significance of all predictor variables from F -tests of nested models with and without the variable of interest. We ran all models in the R programming environment (R Core Team, 2018, version 3.5.1) using the package "lme4" (Bates et al., 2015).

3 | RESULTS

3.1 | Earthworm distribution

Earthworms were the most abundant soil invertebrate, comprising ~90% of invertebrate biomass found during all sampling occasions, while leatherjackets (*Tipula* sp.) were the second-most abundant (Table 2). Combined, earthworms and leatherjackets made up more than 99% of the collected prey biomass. Around 75% of the earthworm biomass was present in the top 10 cm in 2013 and ~85% in 2014 (Table 2). The majority of the earthworm biomass was therefore within reach of female godwits (average bill length 10.6 ± 0.6 cm, $n = 183$ females).

Earthworm biomass in the top 10 cm varied between years and months (Figure 1) but was not related to grassland management intensity (binomial model: $\chi^2 = 2.073$, $df = 1$, $p = 0.150$; gamma model: $\chi^2 = 0.87$, $df = 1$, $p = 0.349$). The difference between years was statistically clear in both the binomial ($\beta_{2014} = 1.43$, $\chi^2 = 22.27$, $df = 1$, $p < 0.001$) and gamma models ($\beta_{2014} = 0.57$, $\chi^2 = 40.36$, $df = 1$, $p < 0.001$). The difference between months, on the other hand, was statistically clear in the gamma model ($\beta_{\text{May}} = -0.24$, $\chi^2 = 7.74$, $df = 1$, $p = 0.005$) but not the binomial model ($\beta_{\text{May}} = 0.05$, $\chi^2 = 0.03$, $df = 1$, $p = 0.853$). The predicted earthworm biomass was therefore 21% higher in March than in May and 95% higher in 2014 than in 2013 (see Table 2, Figure 1).

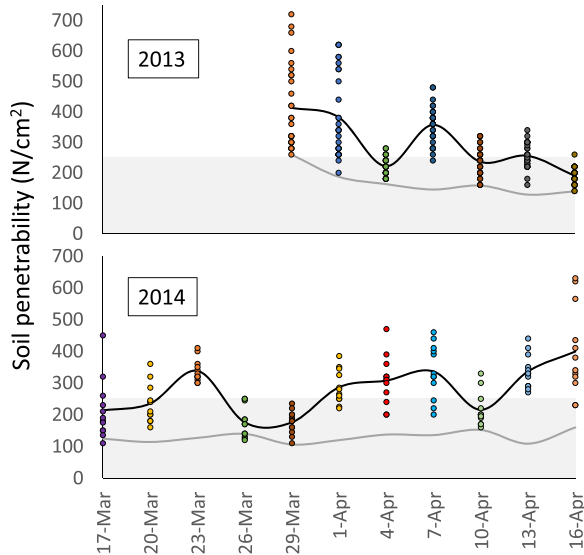


FIGURE 2 Soil penetration resistance during the prebreeding period in 2013 and 2014. The shaded grey area illustrates the range of soil resistance values at which godwit foraging is unaffected by soil resistance ($< 250 \text{ N/cm}^2$; Kleijn et al., 2011). The black line shows the average soil resistance in the high-intensity grasslands and the grey line in the low-intensity grasslands. We have also overlaid the actual values measured at each sampling location throughout the transects in the high-intensity grasslands (dots coloured by sampling date). We did this to illustrate that even though the average soil penetrability was $> 250 \text{ N/cm}^2$, there were sampling locations with $< 250 \text{ N/cm}^2$ in the high-intensity grasslands

3.2 | Soil penetrability

Soil penetration resistance in the high-intensity grasslands was higher than in the low-intensity grasslands (Figure 2). Soil penetration resistance of low-intensity grasslands was consistently lower than the 250 N/cm^2 level suggested by Kleijn et al. (2011) as affecting earthworm availability for godwits (Figure 2). Soil penetration resistance in the high-intensity grasslands was, on average, above this suggested level; however, some sampling locations in the high-intensity grasslands did have a resistance below 250 N/cm^2 (see individual dots in Figure 2).

3.3 | Intake rates, foraging and nesting location

The average godwit intake rate was 1.95 ± 1.03 prey items per minute (range: 0–5.33, $n = 217$, 3 min periods). We observed no clear increase in intake rate with increasing worm biomass (Figure 3). We also did not observe higher intake rates in 2014 when earthworm biomass was 95% higher than in 2013. Instead, we observed low and high intake rates at every sampled earthworm biomass. Accordingly, the fit of the Holling functional response equation to the data was poor (pseudo- $R^2 = 0.06$, $\text{Th} = 24.46 \text{ s}$ (20.98–27.94, 95% CI), $a = 6.45 \text{ cm}^2/\text{s}$ (3.76–10.21, 95% CI)).

We found no clear relationship between the number of foraging godwits in a meadow and the average earthworm biomass in the top

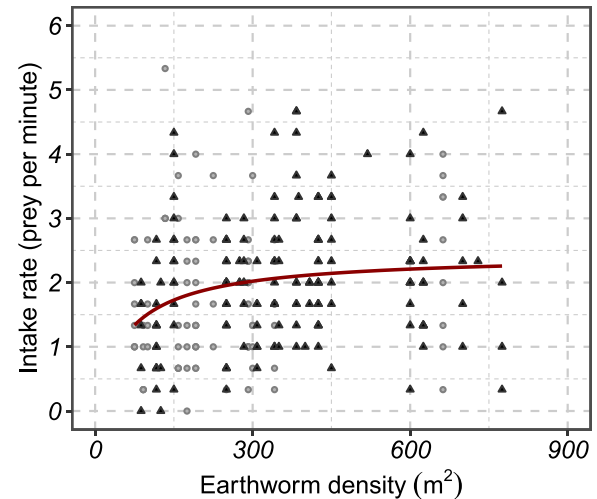


FIGURE 3 Intake rate of female godwits in relation to the earthworm density of the fields in which they foraged in 2013 (circles) and 2014 (triangles). The line represents the best fit of a Holling type II curve to the data

10 cm of that meadow during the pre-breeding period ($\beta = -0.04$, $\chi^2 = 1.16$, $df = 1$, $p = 0.28$; Figure 4, and Figure S2 in the Supporting Information). We did, however, find a *negative* relationship between the number of nests in a meadow and the average earthworm biomass in the top 10 cm of that meadow in March ($\beta = -0.11$, $\chi^2 = 5.74$, $df = 1$, $p = 0.02$; Figures 4 and S2): more nests were found in areas with fewer earthworms.

3.4 | Food availability and decisions on a temporal scale

There was no statistically clear relationship between the arrival dates of individually marked adult female godwits and the average biomass of earthworms during the pre-breeding period in the top 10 cm within 200 m ($\beta = -0.94$, $\chi^2 = 0.43$, $df = 1$, $p = 0.51$) or 300 m of their nests ($\beta = -2.71$, $\chi^2 = 2.32$, $df = 1$, $p = 0.13$). Similarly, there was no statistically clear relationship between the lay dates of individually marked females and the average biomass of earthworms in the top 10 cm within 200 m of their nests ($\beta = 0.07$, $\chi^2 = 0.01$, $df = 1$, $p = 0.94$). However, we did find a *negative* relationship between the lay dates of individually marked females and the average biomass of earthworms in the top 10 cm within 300 m of their nests ($\beta = -3.19$, $\chi^2 = 7.67$, $df = 1$, $p = 0.006$): in areas with more earthworms in the pre-breeding period, females laid earlier. Lastly, we found no statistically clear relationship between the duration of the arrival–laying interval of individually marked females and the average biomass of earthworms in the top 10 cm within 200 m ($\beta = 0.01$, $\chi^2 = 0.005$, $df = 1$, $p = 0.95$) or 300 m of their nests ($\beta = -0.54$, $\chi^2 = 0.12$, $df = 1$, $p = 0.73$).

In the dataset that included all nests found before 1 May, we found no statistically clear relationship between lay dates and the average biomass of earthworms in the top 10 cm within 200 m ($\beta = 0.62$,

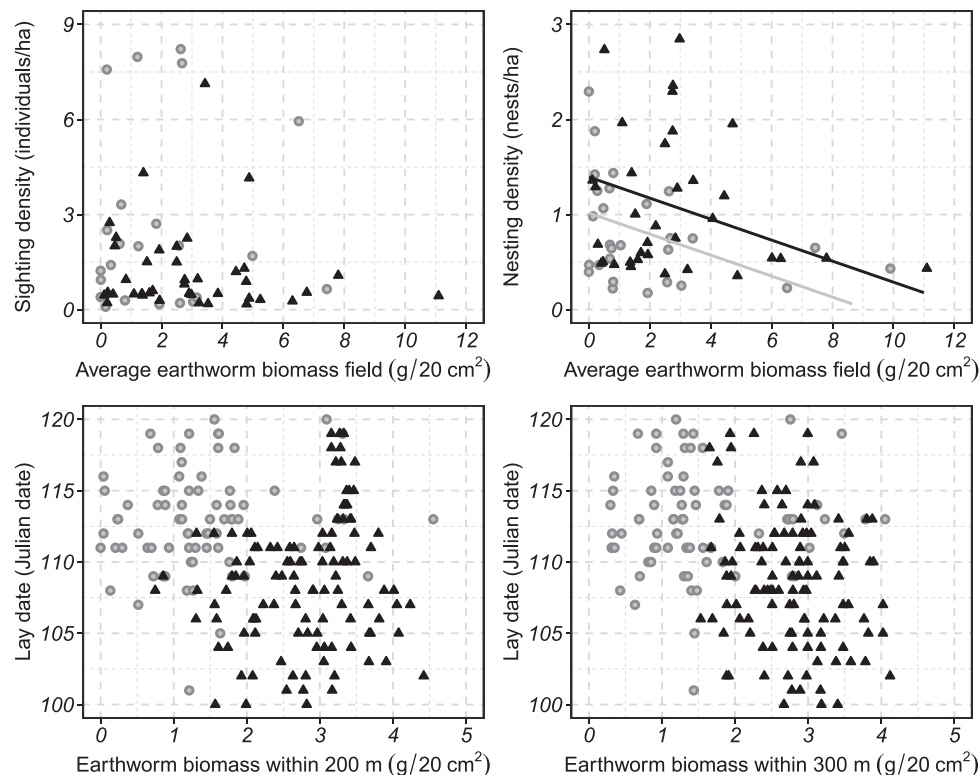


FIGURE 4 Resighting (top left) and nesting density (top right) of godwits on fields plotted against the average earthworm biomass in March in the top 10 cm of soil in those fields. Lay dates of nests in relation to the average earthworm biomass in the top 10 cm of soil within 200 m (bottom left) and 300 m of those nests (bottom right). All four sections of the figure show data from 2013 (circles) and 2014 (triangles)

$F_{1,189} = 3.25$, $p = 0.07$; Figure 4) or 300 m of nests ($\beta = -0.50$, $F_{1,189} = 1.51$, $p = 0.22$; Figure 4). Nor did we find a statistically clear relationship between the average egg volume of nests and the average biomass of earthworms in the top 10 cm within 200 m ($\beta = 0.44$, $F_{1,137} = 2.42$, $p = 0.12$; Figure S3 in the Supporting Information) or 300 m of nests ($\beta = 0.52$, $F_{1,137} = 2.53$, $p = 0.11$; Figure S3).

4 | DISCUSSION

The dramatic population declines exhibited by many of the species occupying European agricultural environments have driven significant interest in identifying management practices that might aid biodiversity conservation (Kleijn & Sutherland, 2003; Potter & Gasson, 1988). Here we investigated whether efforts to promote the abundance of soil-dwelling invertebrates – which can also enhance crop growth – are a viable mechanism to improve the quality of agricultural grassland habitats for the rapidly declining nominate subspecies of the black-tailed godwit. Contrary to previous theory and prevailing management directives (Brandsma, 1999; Högstedt, 1974; Oosterveld, 2006; Van der Weijden & Guldmond, 2006), we found limited evidence that earthworm abundance or availability was correlated with either godwit reproductive timing or breeding density in a polder that has one of the largest concentrations of breeding godwits remaining across the entire range of the subspecies. Our study thus joins a number of other

recent efforts that call into question whether increasing the allocation of nitrogen to agricultural grasslands increases either the availability of food or the quality of those habitats for meadowbirds (Onrust, Hobma et al., 2019; Onrust, Wymenga et al., 2019). Future efforts aimed at halting the declines of godwits and other meadowbirds should instead focus on proven methods, such as controlling the populations of generalist predators (Laidlaw et al., 2021) and restoring water levels in order to slow vegetation phenology, improve soil penetrability, and promote above-ground invertebrate diversity and abundance (Kleijn et al., 2009b; Onrust, Wymenga et al., 2019; Schekkerman & Beintema, 2007; Verhulst et al., 2007).

4.1 | Earthworms and godwit reproductive timing

Previous studies had suggested that low earthworm availability during the godwit pre-breeding period, especially in low-intensity agricultural grasslands, was a likely cause of the mismatch between godwit reproductive efforts and the vegetation and above-ground invertebrate phenology of European agricultural grasslands (Brandsma, 1999; Musters et al., 2010). Accordingly, we predicted that earthworms would be more abundant later in the season and that godwits would nest earlier in areas with higher earthworm abundances during the pre-breeding period. Our results do not strongly support these predictions. Instead, we found that earthworm abundance was higher during the

pre-breeding period and that the vast majority of earthworms were found in the top 10 cm of soil and, thus, available to foraging female godwits. We also found that godwit intake rates were maximized at relatively low densities of earthworms – potentially because of long handling times (Holling, 1959) – meaning that godwit foraging success did not differ across meadows or levels of earthworm abundance. In addition, while we did find a correlation in a subset of our data ($n = 39$ nests) between earthworm abundance within 300 m of a nest and the date on which a female initiated its clutch, this relationship was not apparent in our larger dataset ($n = 192$ nests). Finally, in a separate study (Verhoeven et al., 2020), we found that the amount of time between clutch loss and clutch initiation following nest predation events did not differ across the season, despite declining earthworm availability later in the breeding season. In combination, these results strongly suggest that food availability did not limit godwit reproductive timing and that godwits are capable of finding sufficient quantities of food at low densities of earthworms.

Previous studies in the ecologically similar Northern Lapwing (*Vanelus vanellus*) found a strong relationship between earthworm abundance and the timing of clutch initiation (Högestedt, 1974). Why did we not find such a relationship in godwits? It is possible that the ecological differences that do exist between lapwings and godwits – such as the fact that lapwings feed visually and breed a month earlier than godwits (Baines, 1990) – could explain our contrasting findings. The near-universal cause of phenological mismatches in other systems, however, is the decoupling of the cues used to initiate breeding from those that predict reproductive success (Senner, Stager, & Cheviron, 2018). Unfortunately, little is known about which cues godwits use to time their reproductive events (Lourenço et al., 2011; Senner et al., 2015). More work thus needs to be done to both identify the cues used by godwits to time clutch initiation and to determine how those cues may potentially be managed in agricultural grasslands.

4.2 | Earthworms and godwit settlement decisions

Some studies have proposed that the continued use of low-quality, high-intensity agricultural grasslands by godwits is driven by differences in earthworm abundance during the godwit pre-breeding period (Brandsma, 1999; Hut & Helmig, 2003). Previous work, for instance, has indicated that high-intensity grasslands have higher earthworm abundances (Atkinson et al., 2005; Edwards & Loft, 1982). More recent work, however, has found that soil type – for example, peat versus clay – has a stronger effect on earthworm abundance than management intensity and that the soils of high-intensity grasslands may be desiccated to the point that it reduces earthworm availability (Onrust, Hobma et al., 2019; Onrust, Wymenga et al., 2019).

Our study area included both high- and low-intensity agricultural grasslands, as well as nearly the full range of soil types, nitrogen levels, and earthworm abundances found across the godwit breeding range (Groen et al., 2012; Rutgers & Dirven-Van Breemen, 2012; Teunissen et al., 2012). While we found no relationship between soil type and earthworm abundance (see Onrust, Hobma et al., 2019), our results

generally mirror and extend those of the more recent studies that have called into question the nitrogen-earthworm-godwit paradigm. We found no relationship between earthworm biomass and grassland management intensity. In our sample of high-intensity agricultural grasslands, we found that the soil penetration resistance was often so high that godwits would have a difficult time probing for earthworms (Kleijn et al., 2011). Moreover, we found no relationship between the abundance of earthworms and the density of godwits breeding in an area (see also Baines, 1990). Taken together, our results fail to support the hypothesis that godwits may be continuing to breed in high-intensity grasslands because of food availability.

The continued use of high-intensity agricultural grasslands by significant numbers of breeding godwits may instead be a historical artefact. While godwits are not strictly colonial breeders, they and other species in the genus *Limosa* do form small clusters of nests and these clusters may offer defences against nest and chick predators (Swift et al., 2017). Godwits also exhibit a relatively high degree of nest site fidelity from year to year (Kentie et al., 2014). The combination of conspecific attraction, nest site fidelity, and the high survival rates of adult godwits (Loonstra et al., 2019) could therefore allow godwits to persist in sub-optimal habitats over many years, irrespective of the food availability in those habitats during the pre-breeding period (Hale & Swearer, 2017).

5 | CONCLUSIONS

As the size of dairy farms has grown, so too has the amount of nitrogenous waste they produce (Lord et al., 2002). The potential to apply increasing amounts of nitrogen to the soils of agricultural grasslands, not only to dispose of the nitrogen but also to improve grass growth, increase earthworm abundance, and aid godwit populations, therefore represents an appealing ‘win-win’ scenario. Our results, however, do not support the existence of at least one important linkage in this scenario: the benefits of increased earthworm abundance and biomass for godwit populations. Instead, our results point to the need to implement proven, but more difficult (and controversial) management measures that may help improve habitat quality for godwits more generally; these include restoring and maintaining higher water levels, increasing the botanical diversity of agricultural grasslands, and controlling generalist predator populations. Halting the godwit decline thus must be approached as one part of a complex system. Such complexity does not make finding ‘win-win’ scenarios for farmers and wildlife easy, but it does highlight the need to develop rigorous management plans that are built on sound science rather than easy assumptions. Only when the real costs and benefits to both humans and wildlife are able to be accurately tabulated can we identify true ‘win-win’ scenarios.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

MAV and NRS conceived and designed the study. TP provided all funding. MAV, ADM, and NRS collected the data. MAV performed the analyses. MAV, ADM, and NRS wrote the manuscript with input from all co-authors, who gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.cc2fqz678> (Verhoeven, McBride et al., 2021).

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SUPPORTING INFORMATION

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