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ORIGINAL ARTICLE

Cross-continental differences in Black-tailed Godwit breeding densities are best explained by arthropod abundance in the chick-hatching period

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Abstract
The endangered continental Black-tailed Godwit (*Limosa limosa limosa*) is a migratory ground-nesting wader breeding in a wide variety of open, wet habitats across Europe. Conservation research has concentrated on the causes of population decline, but we know surprisingly little about whether any resources limit local breeding populations and if so, whether these are resources for the adults or the chicks. We collected data from 63 key breeding sites in five countries across Europe to test whether, after correcting for differences in surveyed areas, the size of Godwit breeding populations was related to environmental variables (vegetation biomass, soil moisture) or food resources for adult birds (soil invertebrates) or chicks (vegetation dwelling arthropods) measured during different times of the reproductive cycle. We found the number of Godwit territories to be positively related to arthropod abundance during the chick-hatching period. We found additional, weaker support for a positive relation between Godwit territory numbers and the abundance of soil-dwelling invertebrates (mostly earthworms) at clutch laying, but not at chick-hatching. These relationships were observed across countries, while we found little support for relationships within countries, possibly due to the smaller range in conditions that exist within countries. Both vegetation growth and soil moisture weren't related to Godwit territory numbers. Our results suggest that food abundance for chicks, and to a lesser extent adult birds, are key factors determining the size of local Godwit breeding populations. Conservation management aiming to enhance local Godwit populations should therefore consider the impacts of management strategies on the arthropod prey of chicks.

Keywords Agricultural land-use · Black-tailed Godwit · Arthropods · Habitat selection · Invertebrate availability

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Zusammenfassung

Kontinentale Unterschiede in den Brutdichten der Uferschnepfe lassen sich am besten durch das Vorkommen von Arthropoden in der Zeit des Schlüpfens der Küken erklären.

Die Uferschnepfe (*Limosa limosa limosa*) ist ein ziehender, bodenbrütender Watvogel, der in einer Vielzahl von offenen, feuchten Lebensräumen in ganz Europa brütet. Die Naturschutzforschung hat sich auf die Ursachen des Populationsrückgangs konzentriert, aber wir wissen erstaunlich wenig darüber, ob es irgendwelche Ressourcen gibt, die lokale Brutpopulationen begrenzen und wenn ja, ob es sich dabei um Ressourcen für Altvögel oder Küken handelt. Wir haben Daten von 63 großen Brutplätzen in fünf europäischen Ländern gesammelt, um zu prüfen, ob - nach Ausgleichen der Unterschiede in den untersuchten Gebieten - die Größe der Uferschnepfen-Brutpopulationen mit Umweltfaktoren (Biomasse der Vegetation, Bodenfeuchtigkeit) oder Nahrungsressourcen für Altvögel (im Boden lebende Wirbellose) oder Küken (in der Vegetation lebende Arthropoden), deren Mengen zu verschiedenen Zeiten des Fortpflanzungszyklus erfasst wurden, zusammenhängt. Wir stellten fest, dass die Anzahl der Uferschnepfenreviere positiv mit dem Arthropodenaufkommen während der Schlüpfzeit der Küken zusammenhängt. Ferner fanden wir weitere, schwächere Belege für eine positive Korrelation zwischen der Anzahl der Uferschnepfenreviere und dem Vorkommen von bodenbewohnenden Wirbellosen (hauptsächlich Regenwürmern) zur Zeit der Eiablage, aber nicht des Schlüpfens der Küken. Diese Zusammenhänge wurden länderübergreifend beobachtet, während wir innerhalb der Länder kaum Belege für Zusammenhänge fanden, was möglicherweise auf die geringere Variationsbreite der Bedingungen innerhalb der Länder zurückzuführen ist. Weder die Vegetationsentwicklugn noch die Bodenfeuchte zeigten einen Zusammenhang mit der Anzahl der Uferschnepfenreviere. Unsere Ergebnisse deuten darauf hin, dass das Nahrungsangebot für die Küken und in geringerem Maße für die Altvögel ein Schlüsselfaktor für die Größe der örtlichen Uferschnepfenpopulationen ist. Schutzmaßnahmen zum Erhalt des Bestands und zur Stärkung lokaler Uferschnepfenpopulationen sollten deshalb die Auswirkungen von Managmentmaßnahmen auf die Arthropoden-Beute der Küken berücksichtigen.

Introduction

The continental Black-tailed Godwit (*Limosa limosa limosa*; Godwit hereafter) is a generalist migratory ground-nesting wader species, that breeds in a wide variety of open, wet habitats in Europe (Silva-Monteiro et al. 2021). The largest populations are currently located in intensive agricultural grasslands in northwestern European countries such as the Netherlands and Germany (Thorup 2006; Keller et al. 2021). Smaller and more isolated populations can be found in most European countries, not only in agricultural habitats but also in natural ecosystems such as bogs and fens (Jensen and Perennou 2007; Ławicki and Kruszyk 2011; Strus et al. 2018). Despite the species ability to thrive under a wide range of environmental conditions, it has been declining throughout most of its range in the last half-century (Gill et al. 2007). In the intensive grasslands of the Netherlands, population size decreased by 30% between 2007 and 2015 (from an estimated 47 to 33 thousand breeding pairs; (Kentie et al. 2016)). Similar trends have been observed in less intensively managed, semi-natural grasslands. For example, in the last three decades, Godwits declined by 38% and 85% in Ukraine and Poland respectively (Ławicki and Kruszyk 2011; Strus et al. 2018). Little is known about population trends in natural habitats (Silva-Monteiro et al. 2021). However, studies that examined other wader species that frequently share breeding areas with Godwits also report sharp declines during the last three decades (Fraixedas et al. 2017).

Conservation research has focused on understanding the causes for local Godwit declines, which, in northwestern Europe, have been linked to the direct and indirect impacts of increasing agricultural intensity (Beintema et al. 1995; Roodbergen et al. 2012). Here, high nest and chick mortality due to ever-advancing mowing and grazing dates (Schekkerman et al. 2009; Kentie et al. 2013), dense monocultural vegetation swards disabling Godwit chicks to forage or hide effectively from predators (Schekkerman and Beintema 2007; Kleijn et al. 2010), low water table potentially reducing invertebrate availability for both chicks and adults (De Felici et al. 2019; Onrust et al. 2019), all reduce the reproductive success of breeding pairs (Kentie et al. 2018). In eastern Europe, population decline is predominantly driven by agricultural land abandonment resulting in shrub and tree encroachment that makes many locations unsuitable for Godwits (Leito et al. 2014; Żmihorski et al. 2018; Kamp et al. 2018). Moreover, the predation pressure of both nest and chicks has been increasing across all breeding habitats in Europe, seemingly independent of the intensity of land-use (Silva-Monteiro et al. 2021).

Surprisingly little is known about whether any resources limit the number of breeding pairs of waders in a habitat and if so, whether these are resources for the adults or the chicks (Silva-Monteiro et al. 2021). This is important information if we want to design effective strategies for the sustainable conservation of waders because population size is determined by the product of the habitat area and the breeding density. Godwit breeding densities differ markedly and predictably across habitats with a clear optimum at intermediate land-use intensities where semi-natural grasslands are being managed to enhance productivity somewhat but

Table 1 Model selection and model averaging results for candidate models explaining Godwit breeding population size at the site and country averaged laying date

Predictor	Clutch-laying period model					β	95% CI	ωp
	#1	#2	#3	#4	#5			
Site area within	0.20	0.20	0.18	0.18	0.19	0.19	**0.03 – 0.36**	1.00
Soil invertebrate across	0.35		0.35		0.35	0.20	-0.25 – 0.65	0.56
Arthropod within			0.09	0.09		0.03	-0.10 – 0.16	0.32
Vegetation biomass within					0.05	0.01	-0.06 – 0.07	0.07
ΔAICc	0.00	0.12	1.16	1.21	1.99			
ωm	0.29	0.28	0.16	0.16	0.11			

Candidate models are ranked in order of increasing differences in corrected Akaike information criterion (ΔAICc). Akaike model weights (ωm) indicate the probability that a model is the best-approximating model given the set of models considered. For each predictor, the parameter estimate for each candidate model is given, along with its model-averaged estimate (β) (including zeros for variables that are not in a particular model), 95% confidence interval, and relative importance (ωp). Confidence intervals that do not overlap zero are indicated in bold

are not yet heavily drained, levelled, fertilized and reseeded (Silva-Monteiro et al. 2021). Why breeding densities in natural or extensively managed areas such as mires and coastal and floodplain meadows are so much lower than in the more intensively managed grasslands remains unclear. The population size of waders has been found to be determined by essential resources such as food (Goss-Custard 1991; Zharikov and Skilleter 2003; Piersma 2012; Bakker et al. 2021) although this has almost exclusively been examined in the non-breeding season. Kleijn et al. (2009a) reviewed studies in the Netherlands and Germany examining the relationship between breeding densities on one hand and groundwater level and prey abundance for adult Godwits (e.g. earthworms) on the other and found that settlement densities were more consistently positively related to water level than to earthworm abundance. They speculated that Godwits use soil moisture to select sites that provide good chick-rearing habitat. Wet habitats generally support higher arthropod prey (Eglington et al. 2010; De Felici et al. 2019) and have vegetation structure that is often more open and accessible to chicks (Kleijn et al. 2009b). Identifying the key environmental factors that determine the number of breeding pairs in Godwit habitats can help develop management practices to support and strengthen local populations.

Here we examine which environmental variables are most strongly related to the number of Godwit breeding pairs across a European gradient in land-use intensity. In 63 known Godwit breeding sites located in five countries, we determined local population sizes by means of territory mapping of breeding birds. In each site, we furthermore sampled vegetation biomass, soil moisture content and assessed above- and belowground invertebrate abundances throughout the breeding season. We specifically asked to which environmental variables Godwit territory abundance were most strongly related and whether this differed between the establishment phase (clutch-laying) and the chick-hatching phase.

Methodology

Study sites and design

We collected data in 63 sites in France, the Netherlands, Poland, Estonia and Finland. All sites were areas potentially hosting breeding Godwits, as indicated by survey information from the years before this study was conducted. Site selection aimed to include locations varying widely in environmental conditions both within countries and between countries to incorporate as much variation as possible in variables potentially explaining Godwit breeding numbers and representing all habitat types used by Godwits for breeding (Silva-Monteiro et al. 2021). This included bogs and fens (natural habitats with no agricultural use), coastal and floodplain grasslands (semi-natural habitats that are grazed or mown but do not receive any inputs) and improved grasslands varying in management intensity (no to high fertilizer input; see supplementary online information' Table 1 for more detailed information). We thus used a space for time design that reflects the complete transition from a natural undisturbed Godwit breeding habitat to an intensively managed agricultural one (Silva-Monteiro et al. 2021). Additionally, sites were located in countries that included both the extremes and average latitudes of the species' main breeding distribution (AEWA 2008; Keller et al. 2021). We surveyed and sampled each site in a single season starting approximately two weeks before the estimated mean laying date of Godwit clutches (roughly between March and May) with the sampling period covering 48–72 days, depending

on the country. Logistical constraints forced us to sample different countries in different years with sites in Finland being sampled in 2017, sites in Estonia both in 2017 and 2018, France and the Netherlands being sampled in 2018 and the Polish sites being sampled in 2019. Sites were located a minimum of 0.5 km apart ensuring they represented independent observations and varied in size from 2 to 617 ha (mean: 38 ha). Western European countries (e.g. Netherlands) generally had smaller areas compared to Eastern European countries (notably Estonia). Twelve surveyed sites did not have any Godwit breeding pairs in the year of the survey, possibly due to early-season extreme weather events (e.g. drought). Because the sites' environmental variables still represent important data explaining Godwit site selection we nevertheless included the data from these sites into our analysis.

Surveying breeding populations and determining laying date of Godwit clutches

Godwit breeding populations were estimated by means of a territory mapping approach following Bibby et al. (1992), where observations of territory-indicative behaviour (e.g. pair bond, display, alarm, nests etc.) were recorded on field maps and observations from multiple rounds were clustered into territories. We aimed for five rounds per site, but the final number of rounds ranged between four and six. Eighteen sites were inaccessible in the first sampling round due to flooding and therefore had only four rounds. In the twelve French sites, we decided to extend the surveying and sampling period with one more round resulting in six rounds. Surveys were generally performed using a line transect of parallel lines 200 m apart through the whole surveyed area. To determine the exact phenology of the Godwit breeding season we additionally tried to find as many nests as possible. Once a nest was found, we assessed the laying date following the floatation method of Paassen et al. (1984), for which we used the earliest date of three analyzed eggs. The hatching date was subsequently assessed by adding 28 days to the laying date because Godwits generally lay four eggs in four days and start the average 24.5 day incubation period (here rounded to 25 days) immediately after the last egg is laid (Haverschmidt 1963; Verhoeven et al. 2020). To avoid the inclusion of replacement clutches, we excluded all clutches laid after a country-specific date after which we considered it unlikely that first clutches would still be laid. This date was estimated by adding 44 days to the date the first clutch was found in each country. The 44 day period was based on the period between the earliest clutch and May 1st, the known local date where first clutches are stopped being laid in the Netherlands (Verhoeven et al. 2020).

Surveying environmental conditions

In each site, we surveyed arthropods (aerial and ground-active) and soil-dwelling invertebrate abundance, sampled vegetation biomass and measured soil moisture content at twelve-day intervals throughout the local Godwit breeding season. In each site, the number of sampling rounds was the same as the number of bird survey rounds.

Arthropods (insects and spiders) were sampled using a combination of pitfall traps and sticky traps (Eglington et al. 2010). Aerial insects were surveyed using three yellow sticky boards (10×25 cm, adhesive on two sides; brand Koppert, type Horiver) per site and survey round. Sticky boards were placed vertically in the vegetation with the bottom end approximately 10 cm above the ground surface and spaced 10 m apart. After four days, the traps were removed and individual arthropods counted. Ground-active arthropods were surveyed using three pitfall traps (plastic yoghurt cups, height 125 mm and diameter 85 mm) spaced 10 m apart, that were filled with water and cooling fluid to act as a preservative. A cover raised 60 mm above the pitfall traps protected them from flooding during rainfall. Pitfall traps were open for four days per sampling period and closed with a lid for the remaining eight of the twelve days. Total arthropod abundance (of aerial and ground-dwelling arthropods) per round was considered to be the sum of the three pitfalls and three sticky board traps.

Soil-dwelling invertebrates, primarily earthworms and leatherjackets (Tipulidae larvae) were surveyed by extracting 20 cm wide by 20 cm long by 15 cm deep soil samples from each site using a spade (Kleijn et al. 2011). Because soil macro-fauna is not expected to change much over the season, sampling was done only twice during the breeding season, simultaneously with the first and last arthropod samples. In each field, five samples were taken randomly located in the same general location of the arthropod samples. Per site and sampling round, the pooled number of earthworms and leatherjackets were counted and expressed in number of individuals per m^2 and the average of the two sampling rounds was used in the analyses.

Vegetation biomass (dry weight in g/m^2) was estimated by clipping the vegetation in three 30×30 cm vegetation plots randomly located within 10 m of the arthropod sampling sites and weighing them after drying for two days in an oven at 70 °C. To determine soil moisture content (%), five 15 cm deep soil samples located randomly in the same general vicinity as the biomass samples were taken using an auger. Subsamples were pooled and mixed and fresh weight was determined after which samples were dried at 105 °C for one night to determine their dry weight. Soil moisture content in percentage was calculated as (([soil fresh weight – soil dry weight]/soil fresh weight)*100).

Analytical framework

We investigated how the total arthropod and soil-dwelling invertebrate abundance, vegetation biomass and soil moisture in two separate periods were related to the number of Godwit territories per site. As this gave a better model fit than directly using territory densities, we used as the main response variable the number of territories while statistically accounting for differences between sites in the area surveyed. Additionally, it allowed us to examine whether area-territory number relationships differed between countries. Because it is unknown if adult Godwits select a breeding area because it confers benefits to themselves or to their chicks during the rearing period we ran analyses with variable estimates at the estimated clutch-laying and chick-hatching dates (Fig. 1a). For this, we extracted for each environmental variable an estimate at each site's average clutch-laying date and chick-hatching date. For sites where we did not find any nest, we used the country-averaged clutch-laying date and associated chick-hatching date. For soil moisture content we fitted linear relationships with time and used the model predicted values (Fig. 1b). The advantage of using this approach is that it uses data from all our samples, thus reducing the impact of outliers. We followed the same approach for the arthropod abundance and vegetation biomass sampling but here we used either a linear or quadratic regression (best fit visually selected) from the sampled replicas (Fig. 1c and d). We

used the averaged value of the two soil-dwelling invertebrate abundance samples in the models for both periods since soil-dwelling abundance is expected to only slightly vary during the breeding season. The different sites varied in size and we included site area in our analyses to correct for this.

Statistical analysis

To investigate to which extent the set of environmental variables were related to the number of Godwit territories, we employed generalized linear mixed models and an information-theoretic approach. We chose this approach because we were specifically interested in the relative importance of the different variables and we had no prior expectations about the outcome. In contrast to the more traditional hypothesis testing approaches, information-theoretic approaches present likelihoods that a model or variable is the best model or variable rather than tests of significance. We analyzed two sets of models using the same set of environmental variables: the first with the estimates obtained at the site or country averaged laying dates and the second with estimates obtained at the associated hatching dates. We used country as a random variable and applied the "within-subject centring" procedure (van de Pol and Wright 2009) to disentangle the effects of the explanatory variables within and between countries. Some environmental variables, while not being relevant due to lack of variation within countries, can become relevant
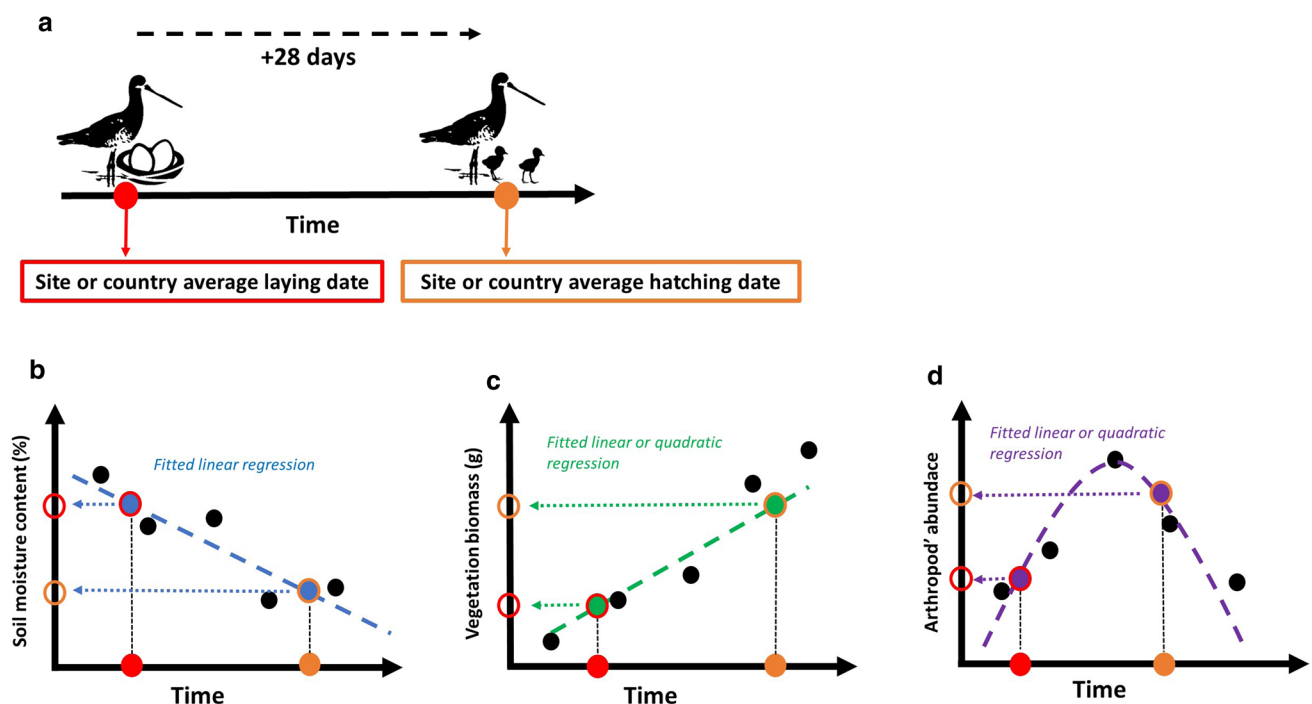

Fig. 1 **a** Methodological process for obtaining estimates of environmental variables at clutch laying and hatching date: **b** soil moisture content, **c** vegetation biomass and **d** arthropod abundance. Country average laying dates were only used in sites without nests

when analysed across a wider geographical range. For this, we first scaled and centred the explanatory variables through the whole dataset to observe potential within-country relations (referred to as "explanatory variable—within"). We also scaled and centred the country's averages of the environmental conditions to observe potential relations across countries ("explanatory variable—across"). We removed variables that were demonstrating multicollinearity by examining the variance inflation factors (VIF; Quinn & Keough 2002; Graham 2003). "Area size—across" was excluded from both sets of analyses and "soil moisture content—across" and "vegetation biomass—within" from the analyses at laying and hatching dates respectively. The remaining explanatory variables all had VIFs lower than 2.5. Interactions between explanatory variables in the models were not considered due to small sample sizes among countries as the analyses across countries are being done based on a single mean value per country. Poisson distribution gave the best fit for both sets of analyses and inspection of residuals suggested none of the models was zero-inflated or suffered from over- or under-dispersion. We used an all-subsets approach to build a model set containing all possible combinations of the different explanatory variables. Given the sample size, individual models were restricted to have a maximum of four explanatory terms, to avoid overfitting (Babyak 2004). We used the Akaike information criterion corrected for small sample size (AICc) to select a candidate set of best models (ΔAICc < 2; Burnham et al. 2011). Full-model averaged parameter estimates (comprising zeroes when the predictors were not present in certain models) were calculated for each predictor in the model set (Symonds and Moussalli 2011). This approach allowed us to compare the relative importance of different predictor variables because standardized

effect sizes of different predictor variables can directly be compared and the 95% confidence intervals of effect sizes can be used to assess their reliability. All analyses were performed in R (R Core Team 2017), using packages glmmTMB (Brooks et al., 2017) and Mu-MIn (Barton 2020).

Results

The results of the analyses at clutch-laying date only provided support for a positive relationship with soil-dwelling invertebrates, such as earthworms and leatherjackets, across countries with a parameter weight of 0.56 and a model-averaged estimate of 0.20 (Table 1). The best model containing soil-dwelling invertebrates indicates an approximately two-fold increase in Godwit territory numbers from sites with the lowest earthworm densities in Finland and Estonia to sites with the highest earthworm densities in the Netherlands (Fig. 2). The 95% confidence intervals of the model-averaged estimate overlapped zero indicating some uncertainty in the support for this variable, but this is perhaps not surprising given that no invertebrates had been observed in near 50% of the sites ($n = 31$) and the many zero values making the analyses less powerful. We additionally found support for the obvious positive relationship between breeding pairs and area size within countries. There was little or no support that godwit territory numbers at clutch laying were related to vegetation biomass, soil moisture or arthropod abundance.

However, at chick-hatching, the arthropod abundance across countries was strongly related to the number of breeding pairs as indicated by the fact that the variable was included in all models in the set of best models (i.e. parameter weight of 1). Furthermore, the model-averaged

Fig. 2 The relationships of the number of Godwit breeding pairs with the soil-dwelling invertebrate abundance across countries, based on the regression plots of the second model of Table 1. The light grey band displays the 95% confidence interval for the shown across-country country relationship. Several site observations are overlapping due to many sites having identical breeding pair counts
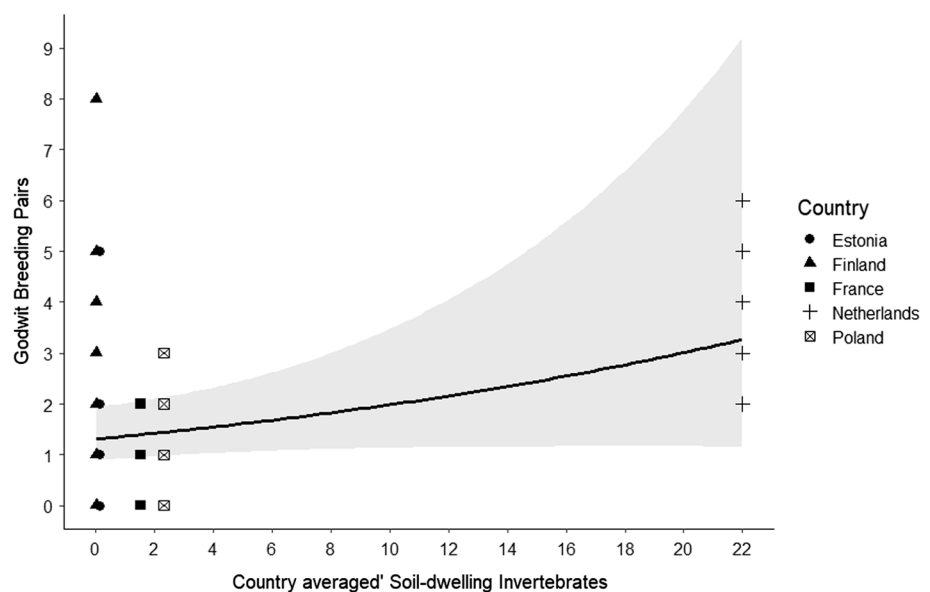
estimate was 0.66 and its 95% confidence interval did not overlap zero (Table 2). An illustration of this relationship based on the model with the lowest AICc suggests a nearly fourfold increase in abundance between sites with the lowest invertebrate abundance (e.g. France and Estonia) and sites with the highest abundance (e.g. Netherlands) (Fig. 3a). Again, results indicate the obvious positive relationship between Godwit breeding pairs and area size but it is noteworthy that its average estimate was three times lower than that of arthropod abundance across countries (Table 2). A graphical illustration of the relationship suggests that the number of Godwit pairs increase with

0.24–0.83 breeding pairs per 10 ha in all countries except for Estonia (Fig. 3b). In Estonia, which had most of the larger surveyed areas that were most often located in bogs and fens, the number of pairs increased only marginally with the increasing size of the surveyed area. Additionally, soil-dwelling invertebrate abundance demonstrated a negative relationship, contrasting with the earlier positive one during the clutch-laying period. However, its −0.19 model-average estimate also overlapped zero. Values for each site's vegetation biomass, soil moisture and invertebrate abundances at the two different explored dates are described in the supplementary tables S2 and S3.

Table 2 Model selection and model averaging results for candidate models explaining Godwit breeding population size at the site and country averaged chick-hatching date

Predictor	Chick-hatching period model				β	95% CI	ωp
	#1	#2	#3	#4			
Site area within	0.20	0.20	0.20	0.22	**0.20**	**0.03 – 0.36**	1.00
Arthropod across	0.70	0.70	0.51	0.70	**0.66**	**0.35 – 0.97**	1.00
Moisture across	-0.22				-0.08	-0.34 – 0.18	0.37
Moisture within				-0.09	-0.01	-0.11 – 0.08	0.14
Soil invertebrate across	-0.28	-0.21		-0.21	-0.19	-0.48 – 0.10	0.78
ΔAICc	0.00	0.56	1.04	1.97			
ωm	0.37	0.28	0.22	0.14			

Candidate models are ranked in order of increasing differences in corrected Akaike information criterion (ΔAICc). Akaike model weights (ωm) indicate the probability that a model is the best-approximating model given the set of models considered. For each predictor, the parameter estimate for each candidate model is given, along with its model-averaged estimate (β) (including zeros for variables that are not in a particular model), 95% confidence interval, and relative importance (ωp). Confidence intervals that do not overlap zero are indicated in bold
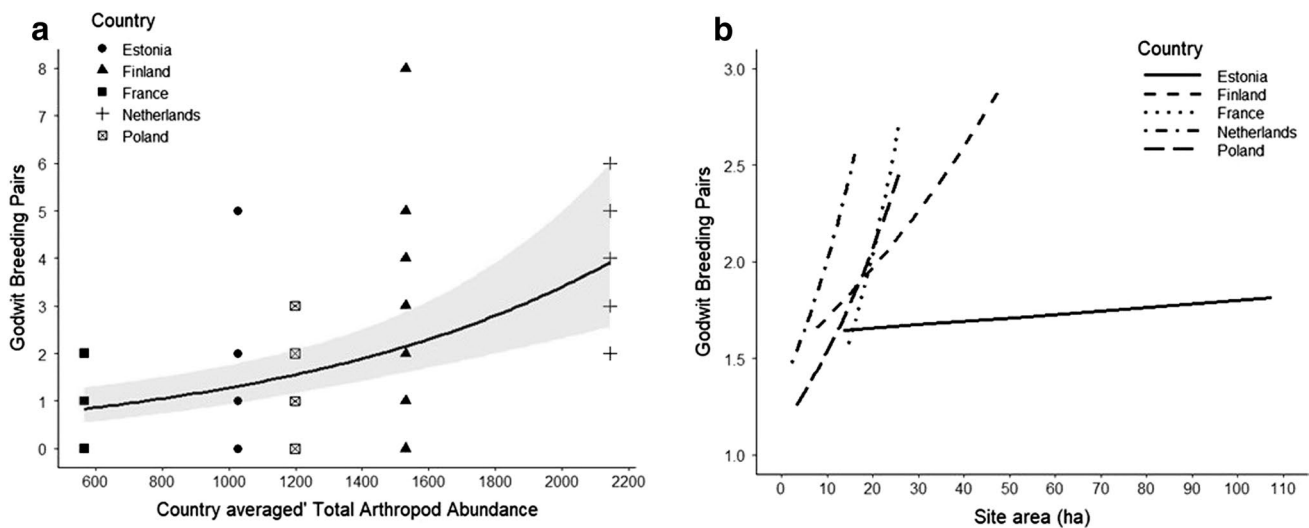

Fig. 3 The relationships of the number of Godwit breeding pairs with total arthropod abundance across countries (**a**) and surveyed area size within countries (**b**). Regression plots are based on the third model on the candidate model list in Table 2. The light grey band of (**a**) displays the 95% confidence interval for the shown across-country country relationship, while several site observations overlapping due to identical breeding pair counts. Confidence intervals and partial residuals are not presented in (**b**) as multiple overlapping confidence intervals would have made the graph difficult to read. For similar reasons of presentation the x-axis of the panel (**b**) was shortened and does include two Estonian sites with surveyed areas of 547 and 616 ha

Discussion

Our cross-continental analysis revealed that soil-dwelling invertebrates in the clutch-laying period and even more so, local arthropod abundance in the chick-hatching period are the best predictors for the number of Black-tailed Godwits breeding pairs. We only found support for relationships with environmental variables across countries with both variables describing food availability. Variables describing the physical conditions of the breeding habitat, vegetation biomass or soil moisture, were found to be far less important or not related to Godwit territory numbers at all.

The positive relationship between the number of Godwit territories and local arthropod abundance at chick-hatching may be explained through two mutually non-exclusive mechanisms. Firstly, breeding pairs may select nest sites that are perceived to be high-quality habitats for their chicks (Kleijn et al. 2009a). Godwit chicks are nidifugous and have to forage for themselves right after hatching. Grassland-dwelling arthropods are the main prey items of Godwit chicks (Beintema et al. 1991; Schekkerman and Beintema 2007) and chick survival immediately after hatching, when chicks are most vulnerable to limitations in food availability (Schekkerman et al. 2009), may be constrained by arthropod abundance. Nest site selection may therefore at least partially be determined by the parent bird's assessment of the abundance of food for their chicks when they hatch. Secondly, arthropod availability may be related, through its positive effect on chick survival, to reproductive success. As far as we know, chick survival is currently the key process driving determining reproductive output throughout the breeding range (Roodbergen et al. 2012; Loonstra et al. 2019). Breeding pairs in sites with more arthropods may be more successful and because Godwits demonstrate natal philopatry (Kruk et al. 1998; Kentie et al. 2014), this may result in higher recruitment rates and therefore larger population size, in sites with high arthropod abundance compared to sites with low arthropod abundance. These two potential mechanisms influencing the population size of breeding Godwits operate at different scales. Site selection will mainly be relevant at local scales as godwits predominantly remain in the region in which they bred before with Godwits in the Netherlands renesting an average of 564 m away from previous years' nest sites (Verhoeven et al. 2020). The potential effect of arthropod abundance on reproductive output will most likely act at a larger, continental scale. Differences in arthropod abundance within habitats are relatively small because they are driven to a large extent by land-use intensity (Silva-Monteiro et al. 2022). The fact that we found support for a relationship with arthropod abundance across countries but not within countries

could then suggest that the mechanism through reproductive output is the dominant factor explaining the patterns in our data (Fig. 3a).

The high relative importance of abundance of soil-dwelling invertebrates, such as earthworms and leather jackets, suggests that food for the adults may be an additional factor determining Godwit breeding densities although to a lower extent. In our study, the high abundance of soil-dwelling invertebrates was mainly restricted to intensively managed grasslands in the Netherlands. However, Leito et al. 2014, observed that within Estonia, with a generally low abundance of soil-dwelling invertebrates, the species often select breeding locations with relatively high earthworm densities. The relationship of godwit territories with prey items for adults may be weaker than that with prey items for the chicks because adult birds are more flexible. For example, Godwits have been found nesting in long-term flooded meadows dominated by sedges that contained only very few prey items of adult birds (Struwe-Juhl 1995). Between incubation bouts, birds were seen foraging up to 500 m from the nest on agricultural lands with high densities of earthworms. The long-term flooding may clear the area of vertebrate prey of potential nest predators (Bellebaum and Bock 2008; Laidlaw et al. 2017) and the benefits of lower nest predation rates may outweigh the costs of larger foraging distances. After the chicks hatch, Godwit families often move to areas where the arthropod availability is higher or more accessible (Schekkerman and Beintema 2007), with adults frequently foraging in different areas when not on guard (Beintema and Visser 1989). The observed negative relationship with soil-dwelling invertebrate at chick-hatching may be the result of the intensive drainage of the most productive grasslands in the Netherlands. The top layer of such grasslands are known to dry out rapidly after which soil-dwelling invertebrates migrate to deeper soil layers where they become inaccessible to Godwits (Onrust et al. 2019). This suggests that sites that combine high soil-dwelling invertebrates at egg-laying with high arthropod abundance at hatching support the highest numbers of Godwit territories.

The somewhat surprising finding that in Estonia the number of Godwit territories was not related to the size of the surveyed area may also be explained by foraging ecology. In many parts of the very large bogs and mires that we surveyed, and that were completely devoid of soil-dwelling invertebrates, adult Godwits may have to fly too far to feed themselves. Here the benefits of safe nesting may no longer outweigh the foraging costs. We may therefore have surveyed areas that seemed suitable to the human eye, but could in fact not support large breeding Godwit populations.

In an earlier study, Silva-Monteiro et al. 2021 found that, across Europe, Godwit breeding densities increase with increasing land-use intensity from natural to moderately intensively managed grasslands. In another study,

Silva-Monteiro et al. 2022 found that the abundance of vegetation-dwelling arthropods and soil-dwelling invertebrates was generally positively related to vegetation productivity, an indicator of land-use intensity. The high availability of vegetation biomass, mostly enhanced by fertilizer input, allows for a more abundant invertebrate community, as it is their primary food source (Haddad et al. 2000; Andrey et al. 2014). Our current study, therefore, suggests that agricultural improvement of (near-)natural habitats has improved the food availability for both adult Godwits and chicks and may thus have increased the carrying capacity of breeding sites. It could explain why Godwits, along with many other wader species, colonized Russian farmland and expanded their range during the course of the twentieth century (Lebedeva 1998) and why Godwits are thought to have increased in population size in the first half of the twentieth century in their current stronghold, the Netherlands (Mulder 1972; Bijlsma et al. 2001). Practices associated with the continued intensification of farming, such as increasingly frequent cutting regimes, the use of dense monocultural swards and removal of within- and between-field relief (Kleijn et al. 2010; Groen et al. 2012; Kentie et al. 2015), are now making modern farming landscapes more and more unsuitable for Godwits, even though they still support abundant arthropod communities (Silva-Monteiro et al. 2022). Our findings, therefore, suggest that moderately managed agricultural grasslands (relatively low fertilizer input, cattle grazing intensities, and extensive cutting regimes and high water tables) offer the ideal breeding habitat for Godwits, as they enhance food availability for both adults and chicks but do not yet have a negative impact on the environmental conditions that enhance chick survival such as proper vegetation cover and high arthropods abundance. Although the exact management practices with which this has to be achieved will have to be tailor-made to each breeding area to take into account inherent differences in, for example, soil type, local hydrology, farming system as well as the impact management will have on other bird species that inhabit the site this means that the optimal conservation management to enhance local Godwit populations should aim for modest increases in land-use intensity at the extensive end of the habitat range, while it should aim for reducing land-use intensity at the intensive end of the range.

Author's Contributions MSM and DK conceived the ideas and designed methodology; MSM, HP, ST, JP, EP, MV, JL, FR, MK, MO, AD, MB, JH and FL collected the data; MSM analyzed the data; MSM and DK led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

References

Andrey A, Humbert J, Pernollet C, Arlettaz R (2014) Experimental evidence for the immediate impact of fertilization and irrigation upon the plant and invertebrate communities of mountain grasslands. Ecol Evol 4:2610–2623. https://doi.org/10.1002/ece3.1118

Babyak MA (2004) What you see may not be what you get: A brief, nontechnical introduction to overfitting in regression-type models. Psychosom Med 66:411–421. https://doi.org/10.1097/01.psy.0000127692.23278.a9

Bakker W, Ens BJ, Dokter A et al (2021) Connecting foraging and roosting areas reveals how food stocks explain shorebird numbers. Estuar Coast Shelf Sci 259:107458. https://doi.org/10.1016/J.ECSS.2021.107458

Beintema AJ, Visser GH (1989) The effect of weather on time budgets and development of chicks of meadow birds. Ardea 77:181–192

Beintema AJ, Thissen JB, Tensen D, Visser GH (1991) Feeding ecology of charadriiform chicks in agricultural grassland. Ardea 79:31–44

Bellebaum J, Bock C (2008) Influence of ground predators and water levels on Lapwing Vanellus vanellus breeding success in two continental wetlands. J Ornithol 150:221–230. https://doi.org/10.1007/S10336-008-0341-7

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav Ecol Sociobiol 65:23–35

De Felici L, Piersma T, Howison RA (2019) Abundance of arthropods as food for meadow bird chicks in response to short- And long-term soil wetting in Dutch dairy grasslands. PeerJ. https://doi.org/10.7717/peerj.7401

Eglington SM, Bolton M, Smart MA et al (2010) Managing water levels on wet grasslands to improve foraging conditions for breeding northern lapwing *Vanellus vanellus*. J Appl Ecol 47:451–458. https://doi.org/10.1111/j.1365-2664.2010.01783.x

Fraixedas S, Lindén A, Meller K et al (2017) Substantial decline of Northern European peatland bird populations: Consequences of drainage. Biol Conserv 214:223–232. https://doi.org/10.1016/j.biocon.2017.08.025

Gill JA, Langston RHW, Alves JA et al (2007) Contrasting trends in two Black-tailed Godwit populations: a review of causes and recommendations. Wader Study Gr Bull 114:43–50

Goss-Custard JD (1991) Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn Estuary. J Appl Ecol 28:1004–1026. https://doi.org/10.2307/2404222

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815. https://doi.org/10.1890/02-3114

Groen NM, Kentie R, de Goeij P et al (2012) A modern landscape ecology of black-tailed godwits: habitat selection in southwest

friesland, The Netherlands. Ardea 100:19–28. https://doi.org/10.5253/078.100.0105

Haddad NM, Haarstad J, Tilman D (2000) The effects of long-term nitrogen loading grassland insect communities. Oecologia 124:73–84. https://doi.org/10.1007/s004420050026

Jensen FP, Perennou C (2007) Management plan for Black-tailed Godwit (Limosa limosa) 2007–2009. Office for Official Publications of the European Communities, Luxembourg

Kamp J, Reinhard A, Frenzel M et al (2018) Farmland bird responses to land abandonment in Western Siberia. Agric Ecosyst Environ 268:61–69. https://doi.org/10.1016/j.agee.2018.09.009

Kentie R, Hooijmeijer JCEW, Trimbos KB et al (2013) Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. J Appl Ecol 50:243–251. https://doi.org/10.1111/1365-2664.12028

Kentie R, Both C, Hooijmeijer JCEW, Piersma T (2014) Age-dependent dispersal and habitat choice in black-tailed godwits *Limosa limosa limosa* across a mosaic of traditional and modern grassland habitats. J Avian Biol 45:396–405. https://doi.org/10.1111/jav.00273

Kentie R, Both C, Hooijmeijer JCEW, Piersma T (2015) Management of modern agricultural landscapes increases nest predation rates in Black-tailed Godwits Limosa limosa. Ibis 157:614–625. https://doi.org/10.1111/ibi.12273

Kentie R, Senner NR, Hooijmeijer JCEW et al (2016) Estimating the Size of the Dutch Breeding Population of Continental Black-Tailed Godwits from 2007–2015 Using Resighting Data from Spring Staging Sites. Ardea 104:213–225. https://doi.org/10.5253/arde.v104i3.a7

Kentie R, Coulson T, Hooijmeijer JCEW et al (2018) Warming springs and habitat alteration interact to impact timing of breeding and population dynamics in a migratory bird. Glob Chang Biol 24:5292–5303. https://doi.org/10.1111/gcb.14406

Kleijn D, Dimmers WJ, van Kats RJM, Melman TCP (2009a) Het belang van hoog waterpeil en bemesting voor de Grutto: I. de vestigingsfase. Levende Nat 110:180–183

Kleijn D, Schekkerman H, Dimmers WJ et al (2010) Adverse effects of agricultural intensification and climate change on breeding habitat quality of Black-tailed Godwits Limosa l. limosa in the Netherlands. Ibis 152:475–486. https://doi.org/10.1111/j.1474-919X.2010.01025.x

Kruk M, Noordervliet MAW, Keurs WJT (1998) Natal philopatry in the Black-tailed Godwit Limosa limosa L. And its possible implications for conservation. Ringing Migr 19:13–16. https://doi.org/10.1080/03078698.1998.9674156

Laidlaw RA, Smart J, Smart MA, Gill JA (2017) Scenarios of habitat management options to reduce predator impacts on nesting waders. J Appl Ecol 54:1219–1229. https://doi.org/10.1111/1365-2664.12838

Lebedeva EA (1998) Waders in agricultural habitats of European Russia. Int Wader Stud 10:315–324

Leito A, Elts J, Mägi E et al (2014) Coastal grassland wader abundance in relation to breeding habitat characteristics in Matsalu Bay, Estonia. Ornis Fenn 91:149–165

Loonstra AHJ, Verhoeven MA, Senner NR et al (2019) Natal habitat and sex-specific survival rates result in a male-biased adult sex ratio. Behav Ecol 30:843–851. https://doi.org/10.1093/beheco/arz021

Onrust J, Wymenga E, Piersma T, Olff H (2019) Earthworm activity and availability for meadow birds is restricted in intensively managed grasslands. J Appl Ecol 56:1333–1342. https://doi.org/10.1111/1365-2664.13356

Quinn GP, Keough MJ (2002) Experimental Design and Data Analysis for Biologists. Exp Des Data Anal Biol. https://doi.org/10.1017/CBO9780511806384

Roodbergen M, van der Werf B, Hötker H (2012) Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: review and meta-analysis. J Ornithol 153:53–74. https://doi.org/10.1007/s10336-011-0733-y

Schekkerman H, Beintema AJ (2007) Abundance of Invertebrates and Foraging Success of Black-Tailed Godwit Limosa limosa Chicks in Relation to Agricultural Grassland Management. Ardea 95:39–54. https://doi.org/10.5253/078.095.0105

Schekkerman H, Teunissen W, Oosterveld E (2009) Mortality of Black-tailed Godwit Limosa limosa and Northern Lapwing Vanellus vanellus chicks in wet grasslands: influence of predation and agriculture. J Ornithol 150:133–145

Silva-Monteiro M, Pehlak H, Fokker C et al (2021) Habitats supporting wader communities in Europe and relations between agricultural land use and breeding densities: A review. Glob Ecol Conserv 28:e01657. https://doi.org/10.1016/j.gecco.2021.e01657

Silva-Monteiro M, Scheper J, Pehlak H et al (2022) Invertebrate abundance increases with vegetation productivity across natural and agricultural wader breeding habitats in Europe. Biol Conserv 273:109670. https://doi.org/10.1016/j.biocon.2022.109670

Struwe-Juhl B (1995) Auswirkungen der Renaturierungsmaßnahmen im Hohner See-Gebiet auf Bestand, Bruterfolg und Nahrungsökologie der Uferschnepfe (Limosa limosa). Corax 16:153–172

Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65:13–21

Thorup O (2006) Breeding waders in Europe 2000. International Wader Studies. https://doi.org/10.5253/078.100.0105

van de Pol M, Wright J (2009) A simple method for distinguishing within- versus between-subject effects using mixed models. Anim Behav 77:753–758

van Paassen AG, Veldman DH, Beintema AJ (1984) A simple device for determination of incubation stages in eggs. Wildfowl 35:173–178

Verhoeven MA, Loonstra AHJ, McBride AD et al (2020) Geolocators lead to better measures of timing and renesting in Black-tailed Godwits and reveal the bias of traditional observational methods. J Avian Biol. https://doi.org/10.1111/jav.02259

Zharikov Y, Skilleter GA (2003) Depletion of benthic invertebrates by bar-tailed godwits Limosa lapponica in a subtropical estuary. Mar Ecol Prog Ser 254:151–162. https://doi.org/10.3354/MEPS254151

Żmihorski M, Krupiński D, Kotowska D et al (2018) Habitat characteristics associated with occupancy of declining waders in Polish wet grasslands. Agric Ecosyst Environ 251:236–243. https://doi.org/10.1016/j.agee.2017.09.033

AEWA (2008) International Single Species Action Plan for the Conservation of the Black-tailed Godwit (TS No. 37) | AEWA. Agreement on the Conservation of African-Eurasian Migratory Waterbirds

Barton K (2020) MuMIn: Multi-Model Inference. R Package version 1.43.17. https://cran.r-project.org/web/packages/MuMIn/index.html. Accessed 8 Feb 2021

Beintema AJ (Albert J, Moedt O, Ellinger D (1995) Ecologische atlas van de Nederlandse weidevogels. Schuyt

Bibby C, Burgess N, Hill D (1992) Bird Census Techniques - 1st Edition

Bijlsma RG, Hustings F, Camphuysen CJ (2001) Algemene en schaarse vogels van Nederland. Avifauna van Nederland, 2.

Brooks ME, Kristensen K, van Benthem KJ, et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9: 378–400. https://doi.org/10.32614/rj-2017-066

Haverschmidt F (1963) The black-tailed godwit. E J Brill, Leiden

Keller V, Herrando S, Voříšek P, et al (2021) European Breeding Bird Atlas 2: Distribution, Abundance and Change. European Bird Census Council & Lynx Edicions, Barcelona

Kleijn D, Dimmers WJ, Kats RJM van, Melman TCP (2009b) De relatie tussen gebruiksintensiteit en de kwaliteit van graslanden als foerageerhabitat voor gruttokuikens. Alterra.

Kleijn D, Lammertsma D, Müskens G (2011) Het belang van waterpeil en bemesting voor de voedselbeschikbaarheid van weidevogels pp. 41–60. SOVON onderzoeksrapport 2011/10

Ławicki Ł, Kruszyk R (2011) Long-term decline of the grassland waders in Western Poland, VOGELWELT.

Mulder T (1972) De Grutto (Limosa limosa (L.)) in Nederland: aantallen, verspreiding, terreinkeuze, trek en overwintering

Piersma T (2012) What is habitat quality? Dissecting a research portfolio on shorebirds. In: Birds and Habitat. Cambridge University Press, pp 383–407

R Core Team (2017) R: A language and environment for statistical computing.

Strus YM, Shydlovskyy IV, Gorban IM (2018) Grassland waders in the upper Prypiat' basin: spatial distribution and number dynamics. "Branta" Trans Azov-Black Sea Ornithol Stn 2018: 53–72. https://doi.org/10.15407/BRANTA2018.21.053