ORIGINAL ARTICLE

A longitudinal study of the effects of trees, geese and avian predators on breeding wader meadow birds: the case of the Demmerik polder, the Netherlands

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Abstract

In the Netherlands, breeding populations of wader meadow birds are in sharp decline. One possible cause is that breeding areas are becoming less open because of tall trees and other factors. The effects of tree lines are generally studied by means of transversal studies spanning a short period of time. We report on a longitudinal field study from 1993 to 2010 into the breeding densities of Eurasian Oystercatcher (*Haematopus ostralegus*), Northern Lapwing (*Vanellus vanellus*), Black-tailed Godwit (*Limosa limosa*) and Common Redshank (*Tringa totanus*) in the Demmerik polder, the Netherlands. One part of this polder, a nature reserve, has an older tree line, while two agricultural parts are divided by a newly developing tree line. As the tree line in the agricultural parts was developing, foraging families of Greylag Goose (*Anser anser*) showed a strong increase in only one of these parts during the breeding season. During the same period, the density of avian predators also increased in the whole polder. Analysis shows waders avoid trees in both situations: with an existing tree line (a static situation) and with a growing tree line (a dynamic situation). We investigated the possible role of geese and avian predators in explaining the decline in density of breeding wader meadow birds, by systematic comparison of several different models. In these models, the effect of the growing tree line has the greatest impact on breeding meadow birds. Models with geese describe the trends of breeding wader meadow birds better than those including avian predators, but since these two variables, geese and avian predators, are confounded, no definitive conclusion can yet be drawn. Potential explanations of and functional mechanisms behind the strong decline in breeding meadow bird populations in this area are discussed.

Keywords Disturbance distance · Interference competition · Meadow bird conservation · The Netherlands · Avian predators

Introduction

Wader meadow bird species like Eurasian Oystercatcher (*Haematopus ostralegus*), Northern Lapwing (*Vanellus vanellus*), Black-tailed Godwit (*Limosa limosa*) and Common Redshank (*Tringa totanus*) are in the threatened category of the European Red List (Birdlife 2015).

The Netherlands is an important breeding area for these species, with over half the European population of the Black-tailed Godwit and about a quarter of that of the Eurasian Oystercatcher breeding here (BirdLife 2017). In the Netherlands, as elsewhere, these meadow bird species are in sharp decline (Teunissen and Soldaat 2005, Koffijberg et al. 2010; Teunissen and Van Paassen 2013; Eugster 2013). For example, the Dutch breeding population of the Black-tailed Godwit (currently estimated at 33,000 pairs) has declined by two-thirds since the 1970s (Kentie et al. 2016).

Several factors are contributing to the sharp decline in meadow bird populations. First of all, the intensification of agricultural practices (Donald et al. 2006; Koffijberg et al. 2010, 2012) as well as traffic (Reijnen et al. 1996; Benitez-Lopez et al. 2010) leads to disturbance and fragmentation of breeding populations and consequently increases their susceptibility to predation (Seymour et al. 2003, Bolton et al. 2007). Second, the decline in openness of the landscape (more tall

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structures, especially trees) favours the avian predators of meadow birds, by providing shelter as well as breeding and perching opportunities (Teunissen et al. 2005; Wallander et al. 2006; Van Der Vliet et al. 2010). Hence, meadow birds tend to avoid tree lines; the Black-tailed Godwit, for example, is quite sensitive, reaching a maximum territory density of 250–600 m from tall tree lines (the so-called disturbance distance), whereas the Eurasian Oystercatcher is less sensitive, with a disturbance distance of about 50 m (Kleijn et al. 2008a; Van Der Vliet et al. 2010). Third, an increase in avian predator populations (e.g. from 7000 to 25,000 pairs of raptors in the last 40 years; see Sovon 2018) is often mentioned as an important cause. Birds such as Common Buzzard (*Buteo buteo*) and Grey Heron (*Ardea cinerea*) are the main avian predators in the daytime, while mammalian predators like Red Fox (*Vulpes vulpes*) prey at night (Teunissen et al. 2005, Teunissen et al. 2008). Recently, wintering and breeding populations of Greylag and Egyptian Goose have exhibited explosive growth in Europe, as a result of agricultural intensification (see BirdLife 2004; Van Der Jeugd et al. 2006; Voslamber et al. 2007; Fox et al. 2010; Lensink 2010; Lensink et al. 2010; Lensink et al. 2013; BirdLife 2017; Avé et al. 2017; Fox and Abraham 2017). These increasing geese populations may well play a role in meadow bird decline (Kleijn et al. 2008b; Kleijn and Bos 2008; Kleijn et al. 2011), though the functional mechanisms remain yet unclear.

The effects of tree lines, geese and avian predators on breeding meadow bird species have been studied in several transversal studies by comparing different areas or using transects during one or several years. A disadvantage of these transversal studies is that spatial differences between areas or parts of transects make it difficult to exclude alternative explanations. Here, we report on a study of the Demmerik polder in the Netherlands, where breeding territory densities of meadow birds and the numbers of adult geese and avian predators were monitored and analysed from 1993 to 2010. In part of the polder, a meadow nature reserve (see Fig. 1), there is a long, existing line of trees along an abandoned (1989) railway track (see Fig. 2). In the adjacent agricultural parts of the polder, a new tree line has developed, with small tree seedlings appearing after 1995, when grazing of the railway borders stopped following track abandonment. In this study area, we therefore have potential impacts of a tree line on meadow birds in a static and a dynamic situation. In the first case, we would expect there to already be an equilibrium of lower densities near the tree line, while in the latter, we would expect the birds to start avoiding the trees as they grow taller. Moreover, a growing number of geese, especially Greylag Goose, started foraging with their goslings in the agricultural northern part of the polder starting in 1986, reaching a maximum of several thousand/100 ha, whereas no geese at all were detected in the southern agricultural part. Besides these breeding geese, a limited number of wintering geese of several

species were always present in the polder from November to April.

This research addresses three questions concerning Eurasian Oystercatcher, Northern Lapwing, Black-tailed Godwit and Common Redshank: (1) How have breeding populations of these wader meadow bird species changed in the nature reserve relative to the existing tree line? (2) How have breeding populations of these wader species changed in the agricultural parts relative to the developing tree line? (3) How have breeding populations of these wader species changed under the influence of a growing number of foraging Greylag and Egyptian Goose, combined with avian predator numbers? For all the three questions, the null hypothesis is that trends will be the same, regardless of the distance from the (developing) tree line or the growing number of geese and avian predators. These analyses can be largely characterized as black box analyses. The possible functional mechanism, especially in relation to the effects of geese on meadow birds, is treated in more detail in the 'Discussion' section.

Materials and methods

Study area, period and major developments

This study took place from 1993 to 2010 in the Demmerik polder (52° 12′ 30″ N, 4° 57′ 00″ E) with an area of c. 360 ha, which is part of a larger polder, Groot Wilnis-Vinkeveen, in the central Netherlands (Province of Utrecht). To the north, the polder is bordered by Lake Vinkeveen, to the east by a rural road with scattered trees and shrubs, especially around several farmhouses, to the south by a rural road and to the west also by a rural road and farmhouses (see Fig. 1). The eastern edge of the village Vinkeveen (c. 10,000 inhabitants) is located 500 m from the northwest corner of the study area.

The western part of the polder is a meadow bird nature reserve, with extensive cattle grazing. The eastern parts have conventional agriculture with meadows for dairy cows. A railway track, abandoned in 1989, divides the polder into a northern and southern half. Four quarters can now be distinguished: a nature reserve north of the railway (abbreviated to Res-N, 48 ha), not included in our study (this quarter was partly used for horticulture and greenhouses); a reserve south of the railway (Res-S, 90 ha); a conventional agricultural quarter north of the railway (Agri-N, 68 ha); and one south of the railway (Agri-S, 150 ha), see Fig. 2. Along the abandoned railway in Res-S, a tall tree line (c. 4–6 m) was already present at the start of the research period. In the eastern agricultural quarters, a new tree line along the abandoned railway started developing after grazing in that area was discontinued in 1995.

To assess the effects of the tree lines, we constructed transects perpendicular to the railway with a length of 600 m and of variable width (Fig. 2). These transects in Res-S, Agri-N

Fig. 1 The Demmerik polder study area, bordered by the thick line. In the middle, running north–south, the high-low water table divides between the nature reserve, west, and agricultural quarters, east

and Agri-S are divided into 'strips' parallel to the abandoned railway. The maximum disturbance distance cited in literature is 600 m (see 'Introduction' section).

In the nature reserve, the groundwater table is 5 to 45 cm below soil surface and in the agricultural quarters 20 to 75 cm below soil surface; see AHN-viewer (2019), see Appendix 1. The soil type is lowland peat ('laagveen').

The most dominant trees are Black Alder (*Alnus glutinosa),* willow (*Salix* spec.), Downy Birch (*Betula pubescens*) and European Rowan (*Sorbus aucuparia*). In 2010 both the existing and the new tree line had a height of 4–6 m (see Fig. 3).

Lake Vinkeveen is a large lake measuring 2.5 × 2.5 km, with plenty of small islands for breeding Greylag Goose. The foraging adult geese increased in number from 37 in 1986 to around 2500 in 2008 and were present only in Agri-N and never seen in Agri-S or Res-S. In the second half of May, they retreat to the Lake for moulting.

Agricultural management is one of the key factors determining the presence and abundance of meadow birds (see 'Introduction' section). We assumed that, given the homogeneity of soil type, water level, landscape structure and

vegetation types and the limited number of farmers active in this area, the agricultural quarters (Agri-N and Agri-S) had very similar agricultural management. As a check, we interviewed two farmers around 2012, each with a major part of their land in Agri-N and Agri-S. We also investigated the agricultural environment schemes (AES) implemented in the period of 2000–2006. These results are described and discussed in online-submitted Appendix 1, Table 3.

Bird counts, preliminary analyses and data management

Breeding meadow birds were monitored according to the guidelines of the Bird Monitoring Project (BMP) of the Dutch ornithological organisation Sovon (Van Dijk et al., updated 2004). During the breeding season, the three quarters studied, Res-S, Agri-N and Agri-S, were visited at least three times, and indications of territorial behaviour and breeding were mapped. The results were then processed using the software AutoCluster, yielding territory numbers and locations of territories in a standardized format (Van Dijk et al. 2012). The presence of other breeding and foraging species (Egyptian
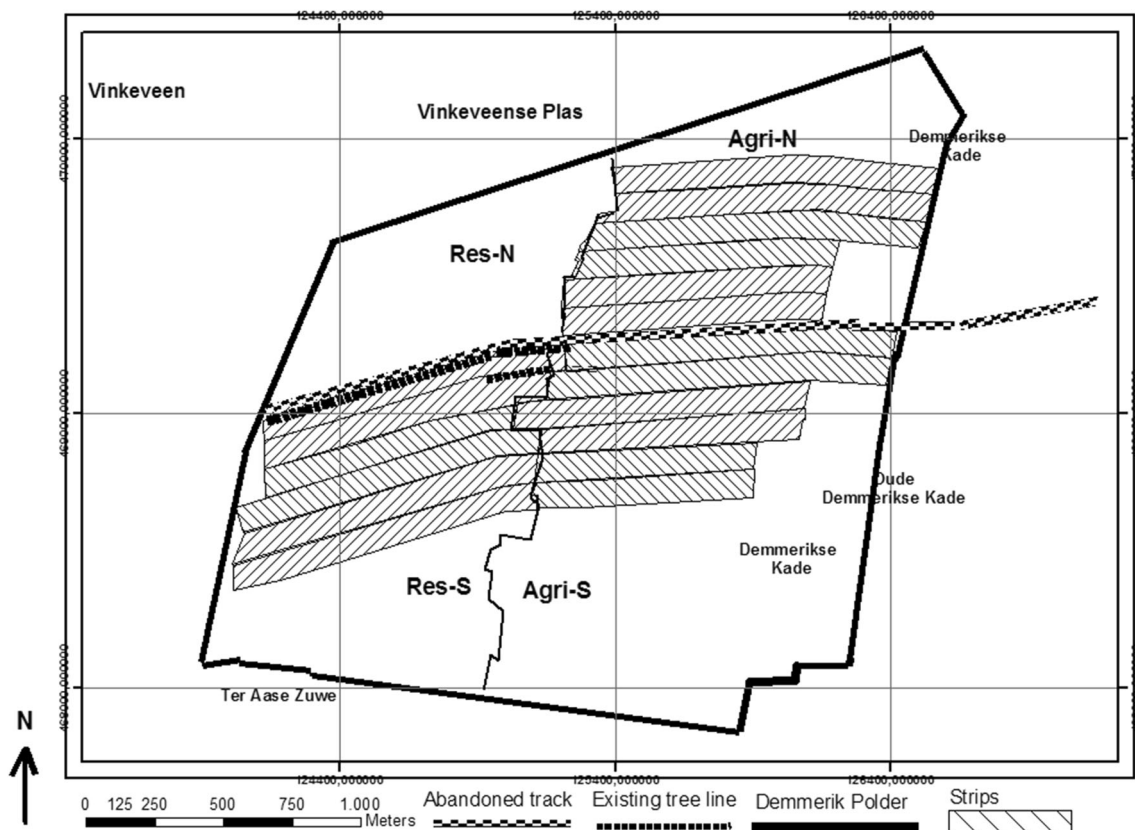
Fig. 2 The six 100-m-wide strips in each quarter of the study area: reserve quarter, south (Res-S) and agricultural quarters north (Agri-N) and south (Agri-S). The strips are used to assess the disturbance distance and effect of the (growing) trees. Also shown the abandoned (1989) railway track, running east–west and, in the reserve, the tree lines at the start of the study

Goose and avian predators) was also counted and/or mapped. During the survey visits, foraging adult Greylag Goose (so not the goslings) were counted (not mapped). The most common breeding avian predators were: Common Buzzard, Eurasian Magpie *(Pica pica)* and Carrion Crow *(Corvus corone)*. Herons and gulls were also counted; for a full list, see Appendix 2, Table 4. There was no systematic observation of mammalian predators. During the whole research period, there were only three observations (anonymous sources) of

the Red Fox, indicating that predation of wader meadow birds in the study area by the Red Fox is probably negligible. Information on numbers and composition of wintering geese was available via Sovon PTT monitoring transects; see Appendix 3.

For further analyses, counts were converted to densities per 100 ha. For the wader meadow birds, the number of territories per year was used, and density was calculated for strips and quarters. For the geese and avian predators, densities in the

Fig. 3 Left: photo taken during removal of sleepers on the abandoned railway track around 1989. Right: photo taken in 2013 from the same position showing the developed tree line (Copyright Cock Willers and heir of Wout Zaal; Heemskerk 2013)

breeding season in each quarter were calculated per year on the one hand and within a year on the other. For the densities per year, the maximum numbers were used, and missing values were calculated using linear interpolation. For the densities within a year, the numbers per 10-day period (8 periods: from 1 April to 20 June) were used. For the wintering geese, finally, the sum of counts at the observation points was used to calculate the densities for Agri-N and Agri-S.

Several preliminary analyses and data management steps were then carried out. For the analysis of static effect of the existing tree line in Res-S, the densities on wader meadow birds six 100 m strips parallel to the railway were used. The calculated disturbance distances on this transect proved not to differ significantly among the four wader meadow bird species, so we lumped the data on them together (Appendix 4, Table 9) for the remainder of the analyses. To simplify analyses of the effects of existing and developing tree lines on the wader meadow birds, the 100-m strips were combined to three 200-m strips per area (Fig. 2).

A second preliminary analysis was on which combinations of geese species or of avian predator species explained the trends in wader meadow birds the best. This resulted in the selection of combined densities of summer Greylag Geese and Egyptian Geese and of all avian predators.

Statistical analysis

We used the statistical programme R (version 3.3.2, Hornik 2016). For all analyses, we used generalized linear models (GLM) and for model comparisons the package MuMin. In all analyses, we used GLM, with a quasi-Poisson distribution. The year-squared term for year in some of these models was needed because densities (especially of meadow waders) exhibited a peak during the study period. Non-significant terms were successively excluded to achieve a minimum adequate model.

For the analysis of the static effect of the existing tree line on meadow birds, we used the combined wader densities/100 ha per 200-m strips in Res-S as response variable and as explanatory variables: strip distance (further referred as distance) to the tree line (factor, three levels), year and year squared (continuous) and the interaction of the latter two with strip distance.

For the analysis of the dynamic effect of the growing tree line along the railway in Agri-N and Agri-S, we used the combined wader densities/100 ha per 200 m strips for each quarter as response variable and as explanatory variables: quarter (factor, two levels), distance (factor, three levels), year and year squared (continuous) and all the interactions between strip distance, quarters and time.

For the analyses of the importance of the growing tree line, geese and avian predators, a two-step procedure was followed.

First, we analysed the trends of geese and avian predators in time and then performed a model comparison.

For the analyses of trends in time of geese, and of avian predators in the agricultural quarters (Agri-N, Agri-S), we combined the geese species, and we combined the avian predators, and took densities/100 ha per quarter as response variable and as explanatory variables: year and year squared, quarter (factor, two levels) and the interaction between time and quarters (see Appendix 2, Table 5, 6).

For the trend analyses of geese species and all avian predator species within a year, the same analyses were repeated, but instead of year, we used an extra single term: 10-day period (continuous, from 1 April until 20 June, eight periods) as explanatory variable.

To determine the respective importance of a developing tree line, geese and all avian predators, we used the R package MuMin, taking the total strip density of wader meadow birds in Agri-N and Agri-S as response variable; these data were log transformed, assuming a Gaussian distribution. All explanatory variables were normalized. We compared the best descriptive model, with quarters, year and year squared and interactions as explanatory variables, with all possible mechanistic models. In these mechanistic models, we used year as a proxy for the growing tree line, and quarter densities of geese species, and all avian predators as explanatory variables. For geese and all avian predators, we had no strip densities, but we assumed their quarter densities are a good enough proxy.

Finally, to enable comparison between trends in meadow wader birds in the study area with those in similar areas, we also calculated the density of each individual species per quarter of the study area. Further explanation of the additional statistical analyses is provided in the Appendix 2 and 3.

We did not account for possible spatial and temporal autocorrelations in our analyses, which might lead to overestimation of the effects. Breeding meadow birds generally exhibit strong site fidelity (Kentie et al. 2014) and of course one strip/quarter looks like the next. Besides the technical complexities of taking autocorrelations fully into account, we would argue that site fidelity and longevity of wader meadow birds will obscure the potential effects of any disturbances and that the densities of strips are inherently correlated, but that setup adopted takes into account the maximum range of effects.

Results

Influence of existing tree line along railway in Res-S

In the minimal adequate model, there is no significant interaction between distance, year and year squared. Thus, trends close to and further away from the tree line along the railway do not differ significantly. The density in the 0–200-m strip is significantly lower than in the two strips farther away

(deviance = 1.29, df = 2, $P \ll 0.001$). The terms year and quadratic year are significant (deviance = 1.07, $P \ll 0.001$, df = 1, respectively, deviance = 0.98, df = 1, $P \ll 0.001$). A maximum is exhibited around 1999, with a density of c. 100 wader meadow bird territories/100 ha near the railway with trees and 140 territories/100 ha further away from the railway; see Fig. 4. The strip densities of wader meadow birds fall by half between the peak year and 2010, a decline of about 5.6%/ year.

Influence of developing tree line along railway in Agri-N and Agri-S

There is no significant three-way interaction between quarters (Agri-N, Agri-S), distance, year and year squared. There is a significant interaction between distance and the quadratic year term (deviance = 57.07, df = 2, $P = 0.025$). Trends in time in the three strips thus differ significantly, regardless of the quarter (Agri-N or Agri-S). There is also a significant interaction between quarter and year (deviance = 132, df = 1, $P \ll 0.001$), so the trends in the two agricultural quarters differ significantly, regardless of the distance; see Fig. 5.

In the strips in Agri-N maximum densities occur around 1995, in the strips in Agri-S around 1997; see Table 1. The decrease in density between the peak year and 2010 in the strip near the railway is by a factor 50 in Agri-N and by a factor 20 in Agri-S. For the strips further from the railway, this decrease is much less: tenfold (Agri-N) and fourfold

(Agri-S). The average decreases for the total strip area in Agri-N and Agri-S are 19.2 and 16.1%/year, respectively.

Trends in geese and avian predator densities in Agri-N and Agri-S

In the study period, the densities of Greylag Goose in Agri-N increased 10-fold, from about 220 to 2200/100 ha (deviance = 7441.8, df = 1, $P < 0.001$) , with no Greylag Goose in Agri-S; see Fig. 6. Egyptian Goose densities are very erratic, with no trend, though the density/100 ha in Agri-N (c. 10) is significantly higher than in Agri-S, by a factor 2.8 (deviance = 241.92, df = 1, $P < 0.001$). The density/100 ha of wintering geese in strips in Agri-N and Agri-S showed a slightly positive, though not significant increase over time. The density/ 100ha of wintering geese in strips in Agri-N and Agri-S showed a slightly positive, though not significant increase over time. The density in Agri-N (c. 39) is not significantly higher than in Agri-S; (c.26), see Appendix 3.

For all avian predators, there was a significant upward trend (deviance = 47.85, df = 1, $P < 0.001$), with a 2.5-fold increase over the period as a whole and no significant differences in trends or differences between Agri-N and Agri-S; see Fig. 6 and Appendix 2, Table 6.

Trends per 10-day period within the breeding season of the wader meadow birds were analysed for Greylag Goose, Egyptian Goose and all avian predators. Besides the aforementioned significant differences (e.g. significant increase of Greylag Goose over time), only the Greylag Goose and avian

Fig. 4 Territory densities per 100 ha of four meadow bird species in strips of Res-S as a function of distance from the existing tree line along the abandoned railway. Lines are modelled densities; symbols are densities based on observations for the same strips
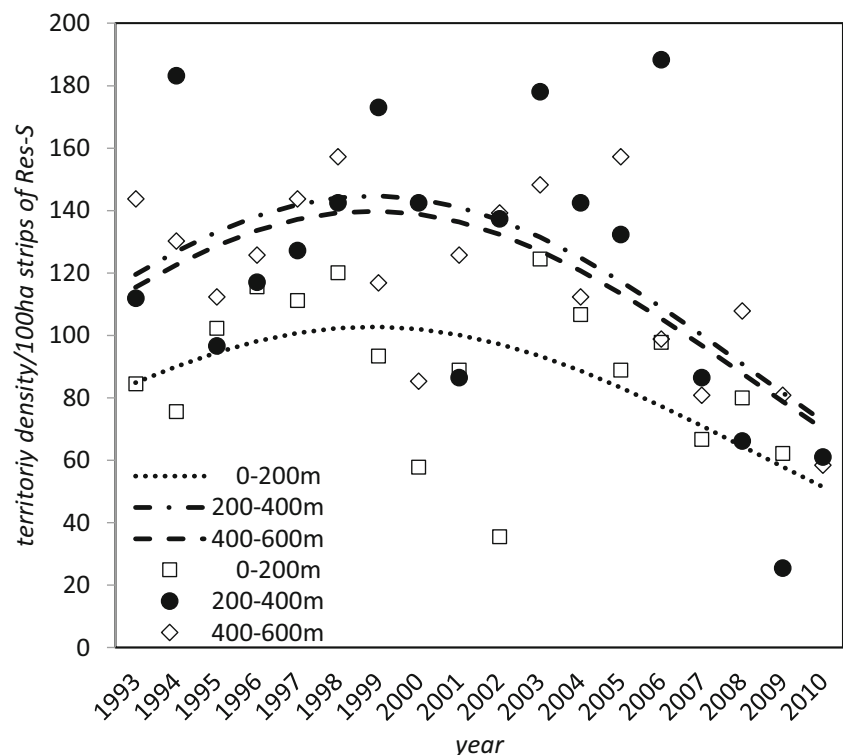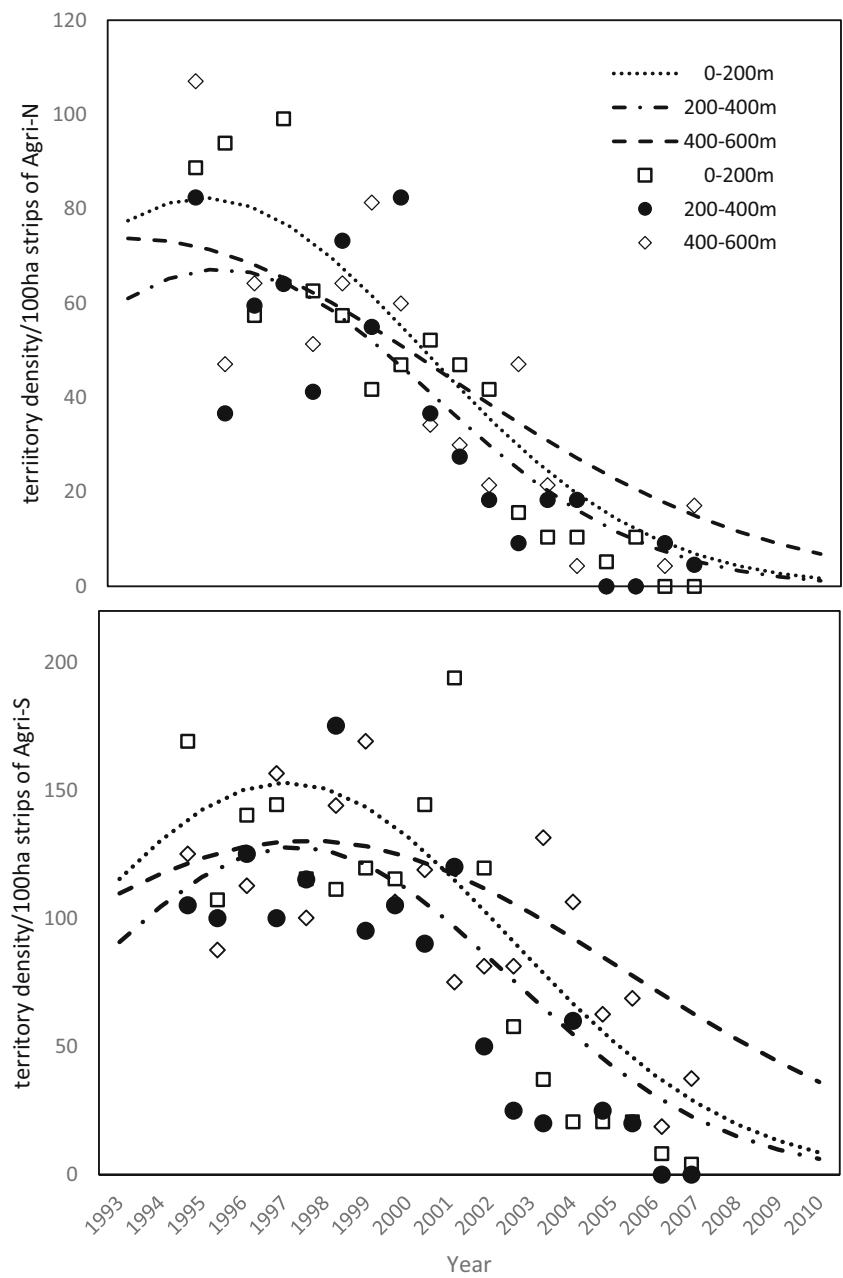
Fig. 5 Territory densities per 100 ha of four meadow bird species in strips of Agri-N (top) and Agri-S (bottom) as a function of distance from the existing tree line along the abandoned railway. Lines are modelled densities; symbols are densities based on observations for the same strips


Table 1 Densities (per strip per100ha) of four wader meadow bird species in the Demmerik polder in Agri-N and Agri-S

Quarter	Agri-N				Agri-S			
strip	*peak year	2010	Factor	%/ year	*peak year	2010	Factor	%/ year
0–200 m	82.3	1.6	50.4	23.0	153.0	8.7	17.6	19.8
200–400 m	67.1	1.2	57.4	23.7	127.8	6.2	20.5	20.7
400–600 m	73.7	6.8	10.8	13.1	130.1	36.2	3.6	10.1

Distance is relative to the abandoned railway. Decrease is calculated as the ratio (factor) and percentage (exponential decrease) per year between peak and last year densities. *Peak year for strips 0–200 m and 200–400 m for Agri-N is 1995 and for Agri-S is 1997; for strip 400–600 m: Agri-N 1993, Agri-S 1998

Fig. 6 Densities (quarter) per 100 ha of Greylag Goose (GG) in Agri-N (left axis) and Egyptian Goose (Egyp) in Agri-N and Agri-S (right axis). Also shown are avian predators (pred) in Agri-N and Agri-S (right axis). Lines are modelled densities; symbols are densities based on observations
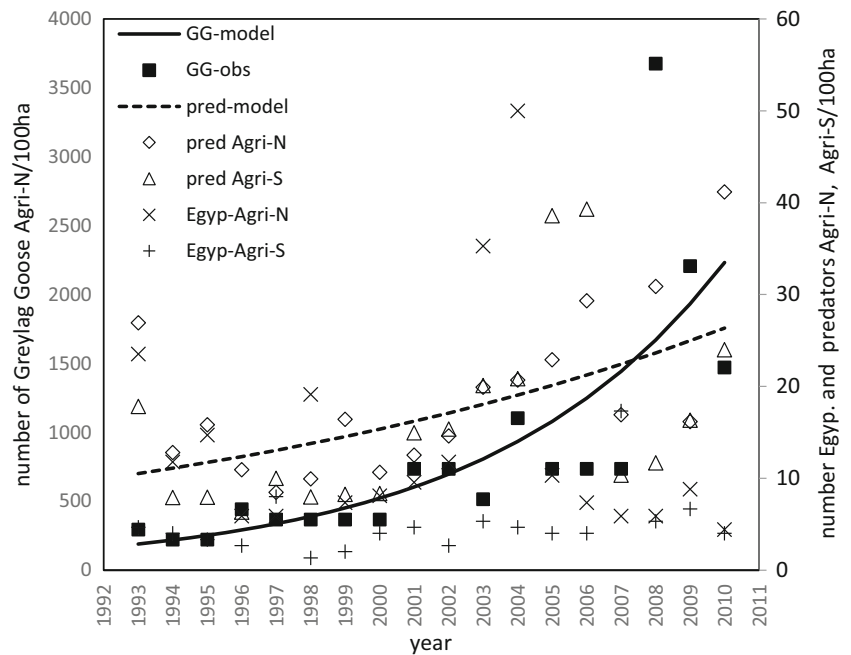
predators showed significant decreases (Greylag Goose, deviance = 1279.9, df = 1, $P = 0.035$; all avian predators, deviance = 151.62, df = 1, $P < 0.001$). The density in the final 10-day period (11–20 June) compared with the first 10-day period (1–10 April) is about 20% for Greylag Goose and 25% for all avian predators.

Combined effect of trees, geese and avian predators

In the previous paragraphs, we described the effects of the growing tree line along the abandoned railway, the increasing numbers of avian predators and the increasing numbers of geese, predominantly present in the northern quarter of the agricultural area. For other factors (like agricultural intensification, soil type, water level), we concluded that these and their trend impacts were the same for Agri-N and Agri-S (see 'Materials and methods' section and Appendix 1).

The similar (increasing) trends for tree line, geese and avian predators mean that these possible explanations are strongly confounded. Since there are differences in trends between the two agricultural quarters, especially for the geese, by comparing different statistical models, we tried to identify the most important factors determining the decrease in meadow bird densities. From Table 2, the best mechanistic model (with tree line, geese and avian predators as explanatory variables) explains less of the variance than the best descriptive model, in the top line of the table. The mechanistic models 2–5 all include the variables tree line (proxy by year) and geese, significant at $P < 0.001$. Avian predators are only significant when present as a single term. The effect of the variable tree line is significantly stronger than that of the variable geese, and the effect of the variable geese is significantly stronger than that of

the variable all avian predators. A reanalysis with the Common Buzzard (as one of the main avian predators) instead of 'all avian predators' showed somewhat stronger effects for this avian predator, but the general conclusions remain the same, see Appendix 2 Table 7.

Discussion

There has been a marked decline in wader meadow birds in all three quarters of our study area, less in Res-S, intermediate in Agri-S and strong in Agri-N; see Appendix 2, Table 8. The Demmerik polder is one the areas of the so-called Lowland Peat Holland region (LVH: Laagveen Holland). Between 1990 and 2010, this region showed an overall decline of about 6% in the four wader species (data provided by Sovon; Heemskerk 2013; Teunissen and Van Paassen 2013). Only in the nature reserve quarter (Res-S) is the decline like the overall decline in the largely agricultural LVH region.

The cause or causes of the stronger declines in the Demmerik polder compared with the LVH region are yet unclear. Do the emerging tree line and rising trends in geese and avian predators make it exceptional? One possible other cause might be that in the second half of the study period, more groundwater was draining from the Demmerik polder to the lower-lying Groot Mijdrecht polder owing to a series of dry springs and summers (oral information, management of Regional Public Water Authority Amstel, Gooi en Vecht). Although this does not affect surface water levels, which are regulated to constant winter and summer levels, it may affect the groundwater table in the middle of the parcels, causing

Table 2　Comparison of models to describe trends in meadow bird (strip) densities in agricultural area (Agri-N, Agri-S) of the Demmerik polder between 1993 and 2010

Int	Q	Year	Y^2	Q:Y	Goose	APr	df	logLik	AICc	Δ	wgt	mod#
3.56	+[***]	− 1.041[***]	− 0.379[***]	+[*]	−	−	6	− 18.41	51.7	−		1
3.72	−	− 0.663[***]	−	−	−0.528[***]	−	4	− 31.70	72.7	0.00	0.781	2
3.72	−	− 0.684[***]	−	−	−0.537[***]	00.048[ns]	5	− 31.62	75.2	2.55	0.219	3
3.72	−	− 0.871[***]	−	−	−	−	3	− 40.95	88.7	15.98	0.000	4
3.72	−	− 0.840[***]	−	−	−	−0.061[ns]	4	− 40.87	91.0	18.35	0.000	5
3.72	−	−	−	−	−0.701[***]	−0.252[ns]	4	− 43.24	95.8	23.08	0.000	6
3.72	−	−	−	−	−0.790[***]	−	3	− 44.68	96.1	23.43	0.000	7
3.72	−	−	−	−	−	−0.500[**]	3	− 52.22	111.2	38.50	0.000	8

Model 1 (mod# 1) is the best descriptive model with Quarter*Year (Q:Y) and quadratic term of year (Y^2). Models # 2 to 8 are mechanistic, with total geese (Goose), group of all avian predators (APr) and tree line (proxy by Y). Values are intercept (Int), regression coefficients (except for factor quarter and interaction quarter:Year). Models ranked by their AICc; df, degrees of freedom; logLik, log-likelihood; Δ, delta, difference from top mechanistic model. wgt, Akaike weight (1.000 for the best descriptive model), + term as factor in model, − term not in model. All variables (Year, Goose, APr) were scaled. All terms were tested for significance by the likelihood ratio test (LRT); ns = not significant (P>0.05), * = P≤0.05, ** = P<0.01, *** = P<0.001

drying out of the upper soil layers and hence limiting food availability (earthworms) for the adult wader meadow birds.

Agricultural management in Agri-N and Agri-S was assumed to be similar; for a further discussion, see Appendix 1. In the following sections, we discuss in more detail the possible importance of existing and emerging tree lines, geese, and avian predators in explaining the decline of meadow wader birds in the Demmerik polder, suggesting possible functional mechanisms as appropriate.

Role of existing and emerging tree lines

We found strong indications that (1) the existing tree line is avoided by wader meadow birds, while distance from it has no effect on trends in breeding numbers; (2) when a new tree line develops spontaneously, wader meadow birds start retreating, at a rate significantly higher closer to the new tree line than further away. Such a dynamic effect of a developing shrub and tree line on breeding densities of wader meadow birds has not previously been demonstrated.

Our findings are supported by several transversal studies analysing disturbance distance in relation to different types of disturbance (Van Der Zande et al. 1980; Reijnen et al. 1996; Wallander et al. 2006; Kleijn et al. 2008a; Benitez-Lopes et al. 2010; Van Der Vliet et al. 2010). Specifically, Kleijn et al. and Van Der Vliet et al. showed that disturbance distances relative to tree lines vary widely between and within wader meadow bird species, from 50 m for Eurasian Oystercatcher to 250–600 m for Black-tailed Godwit. Regarding the functional response, these studies did not specify tree height nor tree use by avian predators (in relation to height). Our study shows a disturbance distance of c. 85 m irrespective of wader meadow bird species. Such a discrepancy might be explained by difference in tree line composition: the trees in our study were 4–

6-m tall, while in previous studies, they may have been far taller (e.g. the poplars, *Populus* spec., typically growing along Dutch meadows easily reach 15–20 m).

Potential role of avian predators

Presence and increased density of avian predators are generally posited as a major explanation for the decline of meadow birds. Teunissen et al. (2005, 2008) cited avian predators as being responsible for a loss of 24–27% of egg clutches and about 20% of tagged chicks (Lapwing and Black-tailed Godwit). In our study area, densities of avian predators are higher in Agri-N (significantly so for the Common Buzzard) than in Agri-S, which might explain the stronger decline of wader meadow birds in Agri-N. Even though our model comparison shows that tree line and geese are much better predictors than avian predators, a supplementary role of the latter cannot be excluded. Besides the direct effects of preying on eggs or young or indirect disturbance by hunting on adult wader meadow birds, there might be also an indirect effect of preying/scavenging on the growing number of goslings. This possible mechanism is supported by the simultaneous decline in the densities of both geese and avian predators throughout the breeding season.

It is well-known that the survival rates of young/eggs are in major decline, while adult survival in these long-living waders remains stable (Schekkerman et al. 2008). Any negative impacts of egg/young predation will therefore not be directly apparent, and immigration (ecological trap) might obscure any adverse effects of any processes. Whatever the case, wader meadow bird populations in the Demmerik polder, the region and the whole of the Netherlands have been in decline for some time, indicating an already long-standing pattern of negative influences.

Potential role of geese

Generally speaking, Kleijn (Kleijn et al. 2008b; Kleijn and Bos 2008; Kleijn et al. 2011; Kleijn et al. 2012) found that wintering or breeding and foraging geese with goslings have no significant impact on meadow birds. Kleijn et al. (2011) reported Greylag Goose densities in nine study areas ranging from 33 to 458/100 ha, which is broadly similar to the densities we recorded in Agri-N from 1993 to 2003 (158–317/100 ha). In our case, though, we did find a negative correlation with breeding wader meadow bird densities. One possible reason may be that in the transversal study of Klein et al., meadow bird densities were not yet in equilibrium (site fidelity of these species) with geese densities, which is not a problem in the case of our longitudinal study.

Swift et al. (2017) posited destruction of waders' nesting habitat through heavy geese grazing as a mechanism. They reported that sharp increases in breeding populations of Snow Goose and Canadian Goose (*Chen caerulescens*, *Branta canadensis*) in the Canada (sub-)arctic exhibited a negative correlation with breeding population size of the Hudsonian Godwit (*Limosa haemastica*). Also, Vickery et al. (1997) found a negative correlation with breeding meadow bird numbers when there were more than 100 wintering geese/100 ha. In our study area, however, wintering geese never reach these densities, although summer geese do (see 'Results' section and Appendix 3). In contrast to the two cited studies, in Denmark Madsen et al. (2019) found no adverse impacts of spring-grazing Barnacle Goose (*Branta leucopsis*) on the nesting densities of the same four wader species as in our study, though there were slightly negative effects for Black-tailed Godwits. It should be borne in mind that meadow bird species differ in their preferred breeding habitats, Northern Lapwings preferring short grasslands, for example (Klomp 1954), so this may be an issue meriting further investigation in our study area. Yet, we have conducted only a few initial analyses, which are presented in Appendix 2, Table 8.

Another mechanism influencing breeding wader meadow birds is interference competition through the aggressive behaviour of parent birds protecting their goslings or simply by their physical presence. For the Egyptian Goose, especially, aggressive behaviour in defending nest sites and young is often mentioned in the popular sources, but this remains unsupported by scientific literature (Anselin and Devos 2007; Gyimes and Lensink 2010; Rehfisch et al. 2010). Kleijn and Bos (2008) showed that Black-tailed Godwits and Northern Lapwings stayed, respectively, 7% and 19% longer on their nest in the presence of geese.

A final possible mechanism by which geese may play an indirect role in wader meadow bird decline might be disturbance by farmers discouraging geese, whether by use of fluttering ribbons on sticks (mandatory to receive government compensation), driving a quad through the meadows or allowing dogs to chase geese. However, as geese only started to be discouraged around 2005–2007 (information from AES project 'De Utrechtse Venen') and these practices occurred only rarely in our study area (see Appendix 1, farmers interviews), they are unlikely to have been a contributing factor during our study period.

Remedial measures

Based on our analysis, the most straightforward recommendations for our study area are as follows: (1) fell the trees in the area to retain the openness of the terrain; (2) take steps to reduce the geese population in the meadow bird areas; (3) undertake ecological research to determine whether interference competition between geese (families) and breeding birds justifies action 2 or advise alternatives; and (4) undertake ecological research on the relationship between geese and avian (and mammalian) predators. In fact, actions 1, along the abandoned railway, and 2 have already been carried out in our study area. In the agricultural quarters of the area, the trees and shrubs along the railway track were cut in 2016, while the Greylag Goose population in the province of Utrecht is being reduced to the damage level of 2005 (Provincie Utrecht 2015). However, these actions will probably not be enough to save the breeding populations of the meadow birds, as the main overriding driver of meadow bird decline is intensification of agricultural practices (see 'Introduction' section).

Recent policy to protect meadow birds in the Netherlands focuses on creating 'core meadow bird areas' (Van 't Veer et al. 2007; Melman et al. 2014; Kuiper 2019). Our study area is part of such an area: the Groot Wilnis-Vinkeveen polder. The Province of Utrecht is devoting major efforts to restoring this area as optimal meadow bird habitat (Provincie Utrecht 2016), through a combination of measures as, e.g. including mosaic management, delayed mowing and grazing and fewer cattle per hectare. To assess the impact of these measures, though that uninterrupted, systematic monitoring is imperative. However, this was continued only after 2016 and then only in a limited way (e.g. only 2 rounds, limited number of species[1]), hampering proper evaluation of the measures.

Analysing trends via a longitudinal case study

Trends in local populations are often governed simultaneously by several different processes acting at different spatial scales. Unravelling the contributions of such processes is generally only feasible by means of a longitudinal study, such as that carried out in our study area, the Demmerik polder, where different processes are occurring in different parts. Despite the strength of longitudinal studies, here too we are faced with

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[1] The four wader meadow bird species in this study plus Northern Shoveler (*Spatula clypeata*)

two entangled processes: geese interference competition and avian predatory effects. Hence, both monitoring and in-depth ecological and behavioural follow-up studies, especially into interactions or competition between meadow birds and geese, are strongly needed in this and other areas.

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