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Sharing habitat: Effects of migratory barnacle geese density on meadow breeding waders

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ABSTRACT

1. Following targeted conservation actions most goose populations have increased. The growing goose populations caused an increase in human-wildlife conflicts and have the potential to affect nature values. As meadow birds, including meadow-breeding waders, were declining throughout Western Europe, the possible negative effect of rising numbers of foraging barnacle geese on their breeding success has been questioned.
2. We used GPS-transmitter data to measure the density of foraging barnacle geese during daylight hours. Using dynamic Brownian Bridge Movement Models (dBBMM), we investigated the effect of barnacle goose density on the territory distribution of five wader species, and on nest success of the locally common Northern lapwing. We used model selection methods to identify the importance of barnacle goose density related to other environmental factors.
3. Our results showed an insignificant positive association between barnacle goose density and nest territory density of the Northern lapwing and common redshank. Barnacle goose density had no influence on territory selection of godwit, oystercatcher and ringed plover. We did, however, find a negative correlation between barnacle geese density and the nest success of the Northern Lapwing.
4. We infer that either barnacle goose foraging leads to improved territory conditions for some wader species, or that both barnacle geese and waders prefer the same type of habitat for foraging and nesting. Higher barnacle goose density was correlated with fewer Northern lapwing nests being successful.
5. *Synthesis and application:* Experimental research is needed to disentangle the causal chain, but based on our observational findings, we suggest to increase water logging that may attract both barnacle geese and wader species. Further investigation on the effects of barnacle geese on wader species is

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necessary to identify the cause of the negative correlation between barnacle geese density and nest success of lapwings; nest protection experiments could give further insight.

1. Introduction

Around the mid-1900s, goose populations in Western Europe had become scarce (Fox & Madsen, 2017). The decline led to the creation of international conservation actions and the development of international legislative frameworks (Stroud et al., 2017). A network of nature reserves and other refuge areas was created, and hunting on a number of populations was restricted or banned in many European countries (Madsen et al., 1999). Following these measures, many of the European goose populations started to increase (Ebbinge, 1991; Stroud et al., 2017; van Roomen & Madsen, 1992). From the 23 recognized goose populations representing 9 species and 13 subspecies, Madsen et al. (1999) found at the time that 14 populations showed an increasing trend, 4 were stable, 2 were decreasing and for 3 populations the trajectories were unknown. At the same time, goose populations started to benefit from agricultural intensification (Abraham et al., 2005; Fox et al., 2005; van Eerden et al., 1996). Geese learned to exploit and forage on modern agricultural farmland, which can provide an unlimited food source during winter and may not be a limiting factor for population growth in the nearby future (Fox & Madsen, 2017).

Grazing, grubbing and trampling by growing goose populations can not only cause an increase in human-wildlife conflicts (Fox et al., 2017) but can also affect a variety of other species (Buij et al., 2017). For example, *Festuca* and *Puccinellia* salt-marshes preferred by mammalian herbivores, such as brown hares *Lepus europeaus,* are also a preferred habitat of socially foraging brent geese (*Branta bernicla*), which can rapidly deplete the resources forcing the mammalian herbivores to move to less preferred foraging sites (Stahl et al., 2006; Van der Wal et al., 1998). Goose grazing also has the potential to affect the suitability of habitat used by breeding wader populations (Smart et al., 2006). Species such as the black-tailed godwit *Limosa limosa*, common redshank *Tringa totanus* and common snipe *Gallinago gallinago* prefer taller vegetation for the nesting phase and during chick rearing (Green et al., 1990; Schekkerman & Beintema, 2007). Intensive foraging by geese could shorten the vegetation to a short and uniform height, which is less preferred by these species of waders during the breeding period (Buij et al., 2017; Kleijn et al., 2011).

Parallel with the increase in population size, some goose species showed a change in behaviour. Barnacle geese *Branta leucopsis* expanded their breeding area towards the southwest and establishing new populations in countries within the Baltic and Nort Sea (Van Der Jeugd et al., 2009).They also delayed their mass spring departure from the Netherlands and Germany from the beginning of April to the middle of May, most likely as a response to increased competition at stop-over sites in the Baltic (Eichhorn et al., 2006). A recent study by Madsen et al. (2022) showed that GPS tagged barnacle geese wintering in farmed areas in Southeast Denmark moved South towards the German Wadden Sea in March and April, prior to their Northward spring migration. This causes a further temporary increase of the barnacle goose population in Northern Germany during late spring, during the period in which large numbers of barnacle geese and breeding waders are both present.

Meadow birds are declining throughout Western Europe (Burfield et al., 2005; Donald et al., 2001; Trouwborst, 2016; Verhulst et al., 2007). The largest decline occurred between 1970 and 1990, but most species are still continuing to decline (Newton, 2004). An important reason for this decline is agricultural intensification (Donald et al., 2001; O'Brien & Smith, 1992; Smith, 1983; Trouwborst, 2016; Vickery et al., 1997). To compensate for this loss of suitable habitat, many countries in Western Europe have created refuge areas, with the intention of bolstering meadow bird populations.

There is an ongoing discussion on the possibility that the increasing goose populations have contributed to the decline of meadow bird populations and particularly of meadow-breeding wader species, but there are only a few empirical studies on this subject. Vickery et al. (1997) showed that fields intensively grazed by dark-bellied brent geese, pink-footed geese *Anser brachyrhynchus* and greylag geese *Anser anser* during winter, support lower and less variable densities of breeding waders during the next summer compared to fields with low grazing intensities. Norris et al. (1998) suggested that the increasing numbers of geese led to an increasing grazing pressure with potentially detrimental effects on suitable habitat for breeding waders. In contrast, Kleijn et al. (2011) did not find a negative effect of wintering greater white-fronted geese *Anser albifrons*, barnacle geese and bean geese *Anser fabalis* on wader populations in the Netherlands. A recent study of Madsen et al. (2019) found no negative effect of intensive grazing by barnacle geese and brent geese on field occupancy by nesting or chick-rearing waders. Tamis and Heemskerk (2020) suggested the possibility of a negative effect of greylag goose density on wader density, but were unable to find strong support for such an effect based on their data and propose further research is needed.

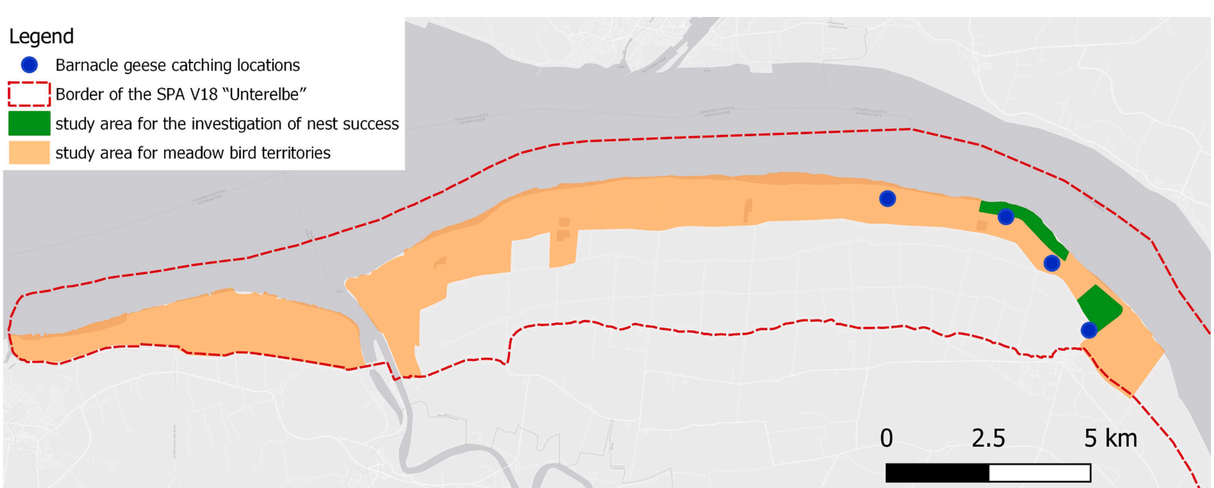

Fig. 1. Study area. (background map: ESRI, 2012)

Previous studies have mainly focused on the effect of geese, during the nest establishment phase of meadow-breeding waders. However, as described by Kleijn et al. (2011), there are three stages in the reproduction of waders that could be affected by growing goose populations: nest establishment phase, incubation phase and chick-rearing phase. The study of Madsen et al. (2019) is the only one, in which the effect of geese on chick-rearing phase was also investigated; no significant influence was found. Our study investigated two hypotheses related to the nest establishment and incubation phases: 1) density of foraging barnacle geese has a negative effect on wader territory distribution, 2) density of foraging barnacle geese has a negative effect on wader nest success.

2. Methods

2.1. Study area and species

Our study area was situated at the mouth of the Elbe river about 20–45 km southeast from Cuxhaven, Germany. The first barnacle geese arrived in September and stayed until the second half of May. Meadow birds started breeding in the second half of March, giving an overlap of almost two months. This made it a suitable area to investigate the influence of barnacle geese on the first two phases of the meadow birds' breeding cycle. We have focused our study on five species of meadow birds present in the area, namely the Northern lapwing *Vanellus vanellus* (hereafter lapwing), the common redshank (hereafter redshank), the Eurasian oystercatcher *Haematopus ostralegus* (hereafter oystercatcher), the black-tailed godwit (hereafter godwit) and the common ringed plover *Charadrius hiaticula* (hereafter ringed plover).

2.2. Meadow breeding waders

Using the standardized territory mapping methods of (2005) we investigated the meadow bird territory distribution within 3,420 ha during the years 2016, 2017 and 2018 (areas marked orange in Fig. 1). Meadow bird nest success was investigated in two extensively used grassland areas (green colour in Fig. 1), with a total area of 115 ha. In the period from 15th March until 30th June, nesting sites were monitored weekly, during the years 2016, 2017 and 2018. Laying dates were either estimated based on the assumption that one egg is laid every day (e.g. in case of two eggs present in the nest, age is 2 days), or it was calculated based on hatching date assuming the mean lapwing breeding period of 27 days (2021). A nest was defined as successful when after a period of around 27 days one or more eggs were hatched. When no eggs were hatched or all eggs were predated, the nest was unsuccessful. Dates were transformed into day number to be able to include them within the model as a numerical variable. The density of nests around a nest often has an influence on its success (MacDonald & Bolton, 2008; Seymour et al., 2003), therefore we analysed nest density as the number of nests within 50 m around the nest that had at least one exposure day overlap with the nest investigated. To investigate nest survival we made use of Mayfield's method that takes into account exposure days, in which exposure days are the total number of days a nest was observed active and therefore under the risk of failure.

2.3. Barnacle goose density

Barnacle geese were caught during the winters of 2015/2016 and 2016/2017 at four sites within our study area (marked by blue dots in Fig. 1). We equipped a subset of 86 caught adult individuals with solar charged GPS (global positioning system) transmitters ("MadeByTheo", Nijmegen). They were attached as a backpack with a Teflon harness (Lameris et al., 2017). GPS positions were collected according to a scheme that is based on the transmitters' battery voltage, with at best, a GPS position every 15 min decreasing down to a GPS position every 6 h. GPS data was collected from 1st April until 31st May during the years 2016, 2017 and 2018. GPS positions were transferred from the transmitter to the database Movebank (https://www.movebank.org) using 2G network.

In order to analyse barnacle geese density, we used a dynamic Brownian Bridge Movement Model (dBBMM) (function: "Brownian. bridge.dyn" in the R-package "move", window size = 31, margin = 13). The model was used to create raster heat maps with a grid cell size of 50x50 m, mapping the density of foraging barnacle geese, later defined as barnacle geese density. A 50 m grid size was chosen because the geese moved on average 0.076 m s^{-1} during our research, which means that they were likely to remain within the same grid cell within these 15 min (i.e. maximum walking distance in 15 min is 68.4 m). Also within the research area barnacle geese often formed large and dense groups and the presence of a single tagged barnacle goose was therefore indicative of the presence of more conspecifics in the immediate surroundings. Next to this, the accuracy of the transmitters GPS is several meters (between 0 and 10 m for 75 % of all positions), so 50 m radius ensures that the GPS point is highly likely within the grid cell.

Absolute numbers of geese were counted weekly between 1st of April and 15th of May to give insight in the general presence and number of barnacle geese present within the research area. We calculated an average of all weekly observation days per year.

2.4. Environmental factors

Based on previous research, four environmental factors were taken into account during this research; 1) waterlogging, 2) ground surface height, 3) distance to nearest field edge, 4) distance to nearest road.

The amount of surface water and moisture are known to influence both breeding waders (Vickery et al., 1997) and grazing density of barnacle geese (Milsom et al., 2002). Therefore we classified each field, which was defined as an area with one crop type bordered by either a fence, ditch or road, based on the number of years with waterlogging (0 = draining, 1 = 10–20 years of waterlogging and 2 = 20–30 years of waterlogging, there were no areas with 0–10 years of waterlogging). Waterlogging was treated as a categorical variable within the statistical analyses.. Ground surface height, was taken from DGM (Digitales Geländemodell; (BfG), 2010) derived from laser scanning in 2010 (10 cm vertical accuracy, 1mx1m resolution). The distance to the nearest field edge was of importance because predators such as the red fox *Vulpes vulpes* prefer to search for prey along field edges (Phillips et al., 2003; St-Georges et al., 1995). The distance to the nearest field edge was calculated using the function gDistance within the R package "rgeos", which enables a researcher to calculate between a GPS position and the nearest line future, which in this research is the fields edge. Using the same method, the distance to nearest road was calculated. This is important because human disturbance is higher when closer to a road (Gill, 1996; Rosin et al., 2012). We analysed the effect of barnacle geese based on only the grassland fields because they provide the main food source of barnacle geese within the area, and thus in these fields a possible effect was most likely to occur. For the nest success analyses we added the estimated laying date as a predictor as this could be of influence on nest success as well (Brandsma et al., 2017).

2.5. Analysis of territory distribution and nest success

To find possible effects of the barnacle goose density and other environmental factors on the territory distribution of waders, we compared observed nest sites from the years 2016 and 2017 with an equal number of random points within the study area (Davis, 2005; Manly et al., 2007). Random points where created within the research area using the function "spsample" from the R package "sp".

To analyse the importance of barnacle geese density and other important environmental factors on wader territory distribution, we applied Binary Logistic Regression models, in which territory presence (0 = random GPS position, 1 = wader territory), was the dependent

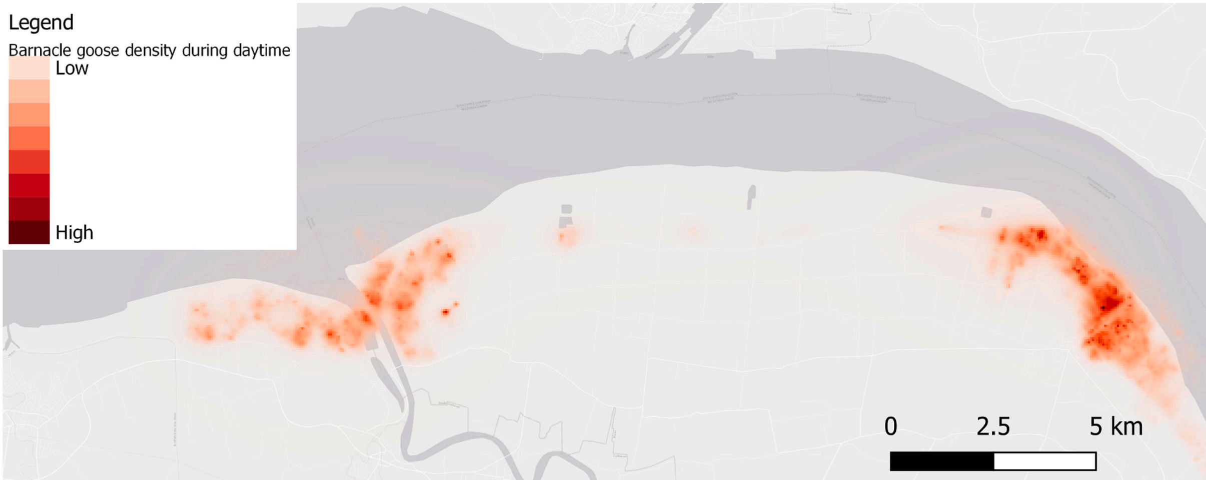

Fig. 2. Barnacle goose density during daytime in the wader nesting season (1st April until 31st May) in 2017 based on GPS transmitter data with a ground speed of < 20 km h^{-1}. A darker red colour indicates a higher density of barnacle geese. Barnacle goose densities during the years 2016 and 2018 can be seen in the Appendix Figs. A.1 and A.3. (background map: ESRI, 2012)

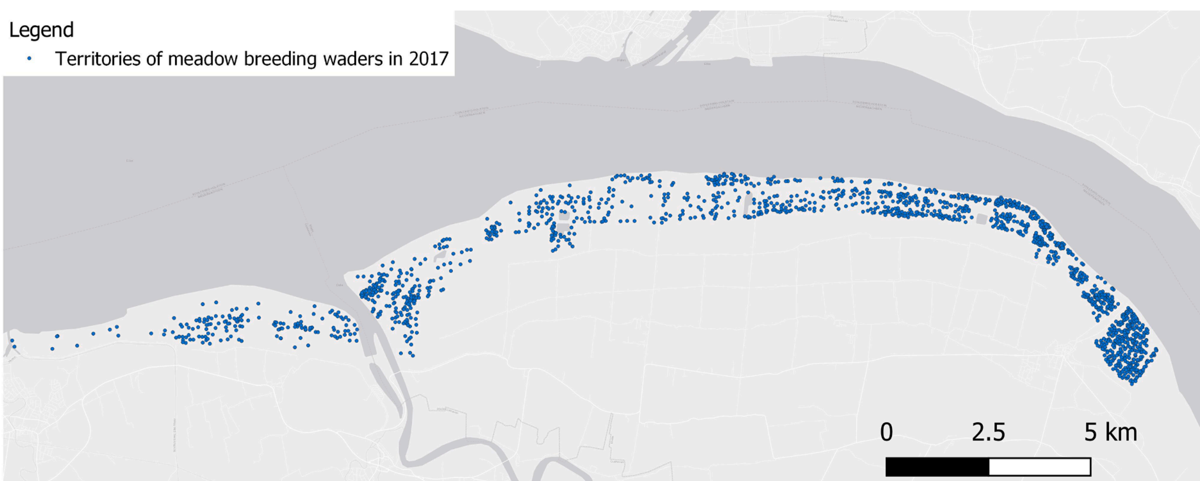

Fig. 3. Territories of meadow breeding waders in the year 2017 (n = 1,772) within the study area marked with blue dots. See Appendix Fig. A.4 for the nest site distribution in 2016. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) (background map: ESRI, 2012).

variable, and barnacle goose density, distance to field edge, distance to nearest road, ground surface height and waterlogging were used as predictors. We investigated the influence of two-way interaction effects between barnacle geese density and distance to nearest field, barnacle geese density and distance to nearest road, barnacle geese density and ground surface height, barnacle geese density and waterlogging and between ground surface height and waterlogging. Interactions where only included when they significantly improved the model with only main effects, according to a Likelihood Ratio Test. Year and field were included as random factors. We used Akaike's Information Criterion scores (corrected for small samples, AIC_c) to identify which Binary Logistic Regression models best fitted the data (Burnham & Anderson, 1998). We assessed multicollinearity using the methods of Zuur et al. (2010). The Variance Inflation Factor (VIF) of the continuous predictors remained below two, for all five wader species.

To analyse the importance of foraging barnacle geese density to other important environmental factors on the nest success of the lapwing we used a Binomial Logistic Regression. We used an adapted model that allows the inclusion of the number of days of exposure (Bolker, 2019), which indicates the number of days that a nest was under research and was under the thread of failure (Mayfield, 1961). We used Akaike's Information Criterion scores (corrected for small samples, AIC_c) to identify which Binary Logistic Regression models best fitted the data (Burnham & Anderson, 1998. Survival of the nest(0 = unhatched or predated, 1 = hatched) was the dependent variable, included predictors were: barnacle goose density, distance to field edge, distance to nearest road, ground surface height, waterlogging, estimated laying date and nest density. Year and field were included as random factors. We investigated the influence of the two way interaction effects between barnacle geese density and distance to nearest field, barnacle geese density and distance to nearest road, barnacle geese density and ground surface height, barnacle geese density and waterlogging, nest density and distance to nearest road, nest density and ground surface height and between ground surface height and waterlogging. Interaction effects where included in the analyses when they significantly improved the model with only main effects, according to Likelihood Ratio Test. Multicollinearity was assessed, the VIF values of the continuous predictors remained below two.

To analyse the relative explanatory importance of barnacle geese density in the statistical models we calculated the AIC_c of all possible candidate models, based on the environmental parameters present in this study (Burnham & Anderson, 1998; Davis, 2005). Taking into

Table 1
Territory distribution models for five wader species. Table includes the top model (lowest AIC_c), and the candidate models with an AIC_c value smaller than two units from the AIC_c value of the top model, and the null (constant) model. The number of parameters (k), delta AIC_c and the AIC_c weights of the models are given. The full model includes the effects of barnacle geese density (BG), distance to the nearest road (DR), distance to the nearest field edge (DF), ground surface height (H), the categorical variable waterlogging (W) and the two-way interaction effects that significantly improved the model including only main effects (based on Likelihood Ratio Test). The dependent variable in each model is nest (N), which can be either 1 = observed nest or 0 = random point.

Species	Model	*k*	*AICc*	*ΔAICc*	*w*
Lapwing (n = 2272)	N ~ DF + H + DR + W + H * W + (1|Field/Year)	10	5443.7	0.00	0.31
	N ~ BG – DF + H + DR + W + H * W + (1|Field/Year)	11	5444.0	0.26	0.28
	N ~ H + DR + W + H * W + (1|Field/Year)	9	5444.7	0.99	0.19
	N ~ BG + H + DR + W + H * W + (1|Field/Year)	10	5444.2	1.44	0.15
	N ~ Constant + (1|Field/Year)	3	5514.9	71.16	0.00
Redshank (n = 631)	N ~ BG – DF + H + DR + W + BG * W + H * W + (1|Field/Year)	13	1571.1	0.00	0.54
	N ~ BG + H + DR + W + BG * W + H * W + (1|Field/Year)	12	1571.8	0.69	0.38
	N ~ Constant + (1|Field/Year)	3	1645.4	74.21	0.00
Oystercatcher (n = 296)	N ~ BG + H + W + (1|Field/Year)	7	810.3	0.00	0.23
	N ~ H + W + (1|Field/Year)	6	810.9	0.57	0.17
	N ~ BG + DF + H + W + (1|Field/Year)	8	811.8	1.48	0.11
	N ~ Constant + (1|Field/Year)	3	821.9	11.58	0.00
Godwit (n = 383)	N ~ BG – DF + W + BG * W + (1|Field/Year)	9	896.0	0.00	0.36
	N ~ BG – DF + H + W + BG * W + (1|Field/Year)	10	897.3	1.27	0.19
	N ~ BG – DF + DR + W + BG * W + (1 | Field/Year)	10	897.6	1.57	0.17
	N ~ Constant + (1|Field/Year)	3	939.1	43.3	0.00
ringed plover (n = 95)	N ~ BG + H + DR + W + BG * DR + BG * W + (1|Field/Year)	11	229.1	0.00	0.29
	N ~ BG + H + DR + W + BG * W + (1|Field/Year)	10	229.9	0.84	0.19
	N ~ BG – DF + H + DR + W + BG * DR + BG * W + (1|Field/Year)	12	231.0	1.95	0.11
	N ~ BG + DR + W + BG * W + (1|Field/Year)	10	231.0	1.98	0.11
	N ~ Constant + (1|Field/Year)	3	249.0	19.97	0.00

account all possible candidate models, we identified which models had an **ΔAICc < 2** and performed conditional model averaging to identify relative explanatory importance of each predictor on the territory distribution of the investigated wader species.

3. Results

3.1. Barnacle goose density

The average number of barnacle geese within the research area (orange in Fig. 1), based on weekly counts during the period between 1st of April and 15th of May, were 29,135 in 2016, 49,600 in 2017 and 94,540 in 2018. Barnacle goose density based on GPS tracked geese was analysed during the wader nesting period from 1st April until 31st May in 2016, 2017 and 2018. During these nesting seasons, 12, 42 and 13 tagged barnacle geese were present, respectively. The distribution of the barnacle goose density based on GPS transmitter data of individual geese was exemplified for the year 2017 (Fig. 2; for 2016 and 2018, see Appendix Figs. A.1 and A.3).

3.2. Territory distribution

In total, we mapped 3,785 wader territories over three years (2016, 2017 and 2018, see Fig. 3 for 2017, Fig. A.4 for 2016 and Fig. A.5 for 2018), within grassland fields. In all years lapwings dominated (2016: n = 857, 2017: n = 741, 2018: n = 674), followed by redshanks (2016: n = 215, 2017: n = 216, 2018: n = 200), godwits (2016: n = 137, 2017: n = 126, 2018: n = 120), oystercatchers (2016: n = 103, 2017: n = 95, 2018: n = 98) and ringed plovers (2016: n = 36, 2017: n = 28, 2018: n = 31).

For the lapwing four models had **ΔAICc < 2**, the top model had a relative explanatory weight of 31 % (Table 1). Model averaging results indicated that the probability of presence of a lapwing territory showed a tendency ($p < 0.10$) to be higher with an increased barnacle goose density and within areas closer to the field edge. The probability of a lapwing territory significantly increased at a higher ground surface height, longer distances from roads and on fields were waterlogging took place, preferably for a longer period of 20–30 years (Table 2). The coefficient of ground surface height was negatively related with areas where waterlogging took place between 10 and 20 years or 20–30 years, thus within fields where waterlogging took place the probability of the presence of a lapwing nest increased at lower ground surface heights.

Territory distribution of the redshank was explained by a top model with a relative weight of 54 % according to AIC_c (Table 1). Two models had a **Δ*AICc* < 2** and were included in the conditional model averaging analysis. The results of model averaging showed a tendency ($p < 0.10$) towards an increased possibility of a redshank nesting territory at areas with a higher barnacle goose density and at smaller distance from nearest field edge. The probability of a redshank nesting territory significantly increased at larger distances from the nearest road, on higher ground surface heights and within areas where waterlogging took place (Table 2). The positive influence of waterlogging increased at lower ground surface heights indicated by the negative interaction effect between waterlogging and ground surface height (Table 2).

Territory distribution of the oystercatcher was best explained by a model with a relative weight of 23 % (Table 1) Model averaging showed that the probability of an oystercatcher nesting territory increased at higher ground surface heights and at fields where waterlogging took place (Table 2).

The top model best explaining territory distribution of the godwit had a relative weight of 36 % (Table 1). Model averaging showed that territory distribution was negatively related to distance to nearest field edge, indicating that the probability of a nesting territory was higher at smaller distance from nearest field edge. The probability of a godwit nest significantly increased at areas where waterlogging took place. In addition, barnacle goose density was positively influenced bywaterlogging, thus the probability of a godwit nest increases at higher barnacle goose densities within areas where waterlogging took place (Table 2).

The best model explaining territory distribution of the ringed plover had a relative weight of 29 %, (Table 1). Model averaging showed that distance to nearest road had a positive significant influence on the presence of ringed plover territories, indicating that areas at shorter distance to roads had a higher probability of the presence of a ringed plover nest (Table 2).

3.3. Nest success

Lapwing nest density within our research area (green areas in Fig. 4

Table 2
Results of conditional averaging of all generalized linear mixed models with ΔAICc < 2 explaining the influence of predictor values on the territory distribution of 5 wader species. Predictors included in the model selection are barnacle geese density (BG), distance to the nearest road (DR), distance to the nearest field edge (DF), ground surface height (H) and the categorical variable waterlogging (W) which is divided into W0 = no waterlogging, W1 = waterlogging for 10–20 years and W2 = waterlogging for 20–30 years. Two-way interactions effects between predictors where also included when they significantly improved the model containing only main effect (based on Likelihood Ratio Test). The dependent variable in each model is nest (N), which can be either 1 = observed nest or 0 = random point.

Species	Variable	Estimate (β)[α]	Conditional $\widehat{SE}_{\beta}$	Z value	2.5 %–97 %	Effect[b]
Lapwing (n = 2272)	*Constant*	−1.77	0.14	12.33	−1.51 to −0.67	***
	BG	0.15	0.09	1.65	−0.10 to 2.07	.
	FE	−0.15	0.18	0.87	−0.57 to 0.05	
	H	0.66	0.19	3.40	0.28 to 1.04	***
	DR	0.78	0.19	4.17	0.44 to 1.15	***
	W1	1.07	0.27	4.00	0.54 to 1.61	***
	W2	0.87	0.28	3.15	0.33 to 1.66	**
	*BG * W1*	0.44	0.63	0.70	−0.79 to 1.66	
	*BG * W2*	−0.81	0.61	1.33	−2.00 to 0.38	
	*H * W1*	−1.94	0.70	2.76	−3.31 to −0.56	**
	*H * W2*	−1.24	0.67	1.85	−2.54 to 0.07	.
Redshank (n = 631)	*Constant*	−1.09	0.22	5.01	−1.51 to −0.67	***
	BG	0.98	0.55	1.78	−0.10 to 2.07	.
	FE	−0.26	0.16	1.65	−0.57 to 0.05	.
	H	0.66	0.19	3.40	0.28 to 1.04	***
	DR	0.78	0.19	4.17	0.41 to 1.15	***
	W1	1.08	0.27	4.00	0.55 to 1.61	***
	W2	0.87	0.28	3.15	0.33 to 1.41	**
	*BG * W1*	0.44	0.63	0.70	−0.79 to 1.66	
	*BG * W2*	−0.81	0.61	1.33	−2.00 to 0.38	
	*H * W1*	−1.94	0.70	2.76	−3.31 to −0.56	**
	*H * W2*	−1.24	0.67	1.85	−2.54 to 0.07	.
Oystercatcher (n = 296)	*Constant*	−0.55	0.18	3.02	−0.90 to −0.19	**
	BG	0.25	0.26	0.96	−0.08 to 0.85	
	FE	0.03	0.09	0.29	−0.20 to 0.46	
	H	0.52	0.19	2.75	0.15 to 0.89	**
	DR	–	–	–	–	–
	W1	0.69	0.25	2.73	0.19 to 1.18	**
	W2	0.86	0.23	3.76	0.41 to 1.31	***
Godwit (n = 383)	*Constant*	−2.26	0.46	4.93	−3.15 to −1.36	***
	BG	−0.84	1.19	0.70	−3.18 to 1.50	
	FE	−0.54	0.23	2.30	−1.00 to −0.08	*
	H	0.24	0.27	0.88	−0.29 to 2.89	
	DR	0.19	0.28	0.70	−0.35 to 0.74	
	W1	2.36	0.53	4.42	1.31 to 3.41	***
	W2	0.74	0.49	3.55	0.78 to 2.70	*
	*BG * W1*	2.60	1.30	2.01	0.06 to 5.14	
	*BG * W2*	0.42	1.26	0.33	−2.06 to 2.89	
ringed plover (n = 95)	*Constant*	−9.25	4.87	1.90	−18.79 to	.
	BG	−26.35	16.24	1.62		
	FE	−0.33	0.58	0.58		
	H	1.14	0.62	1.83		.
	DR	1.58	0.73	2.17		*
	W1	8.84	4.85	1.82		.
	W2	9.53	4.92	1.94		.
	*BG * DR*	3.47	2.20	1.58		
	*BG * W1*	29.67	16.38	1.81		.
	*BG * W2*	27.07	16.26	167		.

and Fig. 1.) was high, on average 112 breeding pairs per square kilometer (2016 = 102 BP/km^2; 2017 = 128 BP/km^2; 2018 = 106 BP/km^2). The effect of barnacle goose presence on the nest success was only investigated for lapwings, due to the small number of nests of the other wader species. We were able to identify the nest success of 193 nests in 2016, 165 nests in 2017 and 137 nests in 2018, within the two investigated areas (Fig. 4). We recorded an overall hatching probability of 0.41 in 2016, 0.52 in 2017 and 0.46 in 2018.

As shown in Table 3, the best model explaining nest success of the lapwing had a relative weight of 23 %. The results of the conditional model averaging (Table 4) showed that there was a negative correlation between barnacle geese density and the nest success rate of the lapwing, which is negatively influenced by the ground surface height as indicated by the significant interaction effect between barnacle geese density and ground surface height. Thus, the negative effect of barnacle geese density is greater at lower ground surface heights.

4. Discussion

Our analysis did not provide any support for the idea that the presence of high densities of barnacle geese during the nesting phase of meadow-breeding waders result in lower number of territories in these species. Rather, nest territory density of lapwings and redshanks showed a tendency to be higher in areas with higher barnacle goose density. However, our results suggest a negative correlation between barnacle geese density and the nest success of the lapwing.

4.1. *Territory density*

In line with our results, Kleijn et al. (2011) found a positive insignificant relationship between the greylag goose density and nesting density of the lapwing. Our study also found a positive association of barnacle geese density and redshank territory selection, which was not found in the study by Kleijn et al. (2011). The oystercatcher, godwit and

Fig. 4. Lapwing nest sites of which nest success was identified for the years 2016 (blue dots, n = 193), 2017 (red dots, n = 165) and 2018 (yellow dots, n = 137). (background map: ESRI, 2012)

Table 3
Nest success models for the lapwing. Table includes the top model (lowest AIC_c), the candidate models with an AIC_c value smaller than two units from the AIC_c value and with fewer predictors than the best model, and the null (constant) models. The number of parameters (k), delta AIC_c and the AIC_c weights of the models are given. The full model included the effects of barnacle geese density (BG), distance to the nearest road (DR), distance to the nearest field edge (DF), ground surface height (H), the categorical variables waterlogging (W), estimated laying date (LD), nest density and the interaction effects between barnacle geese density and ground surface height and between barnacle geese density and waterlogging. The dependent variable was nest survival (S), which could be either 1 = successful nest or 0 = unsuccessful nest.

Species	Model	*k*	*AICc*	Δ*AICc*	*w*
Lapwing (n = 495)	S ~ BG − H + ND − LD + W − BG*H + BG:W + (1|Field/Year)	10	920.8	0.00	0.23
	S ~ BG − H − LD + W − BG*H + BG:W + (1|Field/Year)	9	921.6	0.77	0.16
	S ~ constant + (1|Field/Year)	3	932.4	11.61	0.00

ringed plover were not influenced during their territory selection by the density of barnacle goose within our research area.

In contrast with our study, a negative effect of wintering geese on nest density of waders was found by Vickery et al. (1997). This negative effect might be caused by wader preference for wetter fields. Whereas on their study site the geese had a preference for drier grassland fields, in our study both waders and geese were very active within the areas where waterlogging took place. Another explanation could be that Vickery et al. (1997) investigated the effect that geese have during winter on waders during spring, while our study investigates the effect of barnacle goose density during the nesting period itself. Finally, Vickery et al. (1997) studied dark-bellied brent and pink-footed geese, and it cannot be ruled out that waders respond differently to these other goose species. More recent studies of Madsen et al. (2019) also did not find any negative effect of intensive grazing by barnacle geese and brent geese on the field occupancy of nesting or chick-rearing waders. Waterlogging had a positive influence on the territory distribution of lapwing, redshank, oystercatcher and godwit. For ringed plover, the influence was insignificant but showed a tendency towards a positive influence of waterlogging. Milsom et al. (2002) found that the lapwing and redshank tended to nest closer to wet rills and suggested that breeding lapwings and redshanks could be attracted by flooding rills during April and May. In our study, the number of wader territories was higher in areas with many flooded rills and active waterlogging. Ground surface height showed a positive correlation with the territory distribution of the lapwing, redshank, godwit and a positive tendency with

Table 4
Results of conditional averaging of all models investigating the effect of barnacle geese density (BG), estimated laying data (LD), distance to nearest road (RD), distance to nearest field edge (FE), presence of waterlogging (W), ground surface height, lapwing nest density, the interaction between barnacle geese density and ground surface height (BG*H) and the interaction between barnacle geese density on waterlogging (BG*W) on the survival of Lapwing nest until hatching taking into account the days of exposure of the nests.

Species	Variable	Estimate $(\beta)^{\alpha}$	Conditional $\widehat{SE}_{\beta}$	Z value	2.5 %–97 %	Effect[b]
Northern Lapwing (n = 495)	Constant	4.04	0.54	7.54	2.99 to 5.09	***
	BG	−0.61	0.28	2.21	−1.15 to −0.07	*
	FE	–	–	–	–	–
	H	−0.17	0.23	0.73	−0.61 to 0.28	
	DR	–	–	–	–	–
	W_{no}	39.2	20.3	1.9		.
	ND	0.34	0.21	1.64	−0.07 to 0.75	
	LD	−0.01	0.01	1.51		
	BG * H	−1.24	0.45	2.75	−2.12 to −0.36	**
	BG * W_{no}	82.01	42.16	1.95	−0.60 to 164.65	.

the ringed plover. A possible explanation for this, could be a higher visibility of the surrounding as a protective mechanism against predators. As found by Van Der Vliet et al. (2008), waders prefer an open field to increase visibility as a predator avoidance strategy. Another explanation is that because they prefer fields where waterlogging takes place, it might be necessary to pick areas that are higher to avoid flooding of the nest.

Although known to influence nest site selection of meadow-nesting wader species, we did not measure grass sward height (Devereux et al., 2004; Vickery et al., 2001). Grass sward height on agricultural fields is mainly influenced by either grazing or mowing activities. However, within our study areas, cattle grazing density is kept very low (<2 cattle per ha) and mowing on most fields is only allowed after hatching of the waders. All fields with waterlogging are only mowed after wader fledging. Thus, grass height prior to hatching at these areas is mostly influenced by the barnacle geese density, and therefore indirectly included in our analysis through barnacle geese density. Barnacle geese aggregate during spring, before departure (Buitendijk et al., 2022), the reason for this is likely that they are only then able to cope with the increased grass sward growth in this period as shown in brent geese (Bos et al., 2004). For this reason, we were especially interested where barnacle geese mainly grazed during the period from 1st of April until 31st of May. The high number of barnacle geese within our area keep the sward height to very low levels during winter and on specific fields during spring until their departure around mid-May and waders might benefit from this. The lapwing for example is known to prefer short sward heights (Evans, 2004), while oystercatchers were not negatively influenced by short sward heights as long as predation is low (Van der Wal & Palmer, 2008).

The insignificant positive association between high goose density and density of meadow breeding waders that we found might be due to a shared preference for certain fields, which may mask negative effects of high densities of geese on waders. However, these effects may become apparent when comparing trends in nesting densities over a longer period. In order to investigate this further research is needed. This research should not only investigate if areas with high barnacle geese density show a faster decrease in the number of wader nesting territories and successful nests when compared to areas with low barnacle geese densities, but also compare wader areas with and without the presence of barnacle geese. However, wader nests were only found where barnacle geese foraged, meaning such a comparison could not be made.

4.2. Nest success

The average nesting densities of lapwings in our research area was high (average 112 BP/km^2), which is higher than the mean densities in other wader areas in Lower Saxony (Onnen & Zang, 1995). However, a direct comparison with densities given by Zang et al. (1995) is not appropriate, as their study covers larger areas up to 100 km^2 where our study area consisted of 32 km^2. Densities given by them were within much larger areas (5–100 km^2). With densities of 112 pairs per km^2, we can assume that our research area consisted of optimal breeding habitat for lapwings, and therefore was suitable for research on nesting success. Within our research area there was colonial breeding, which is a possible

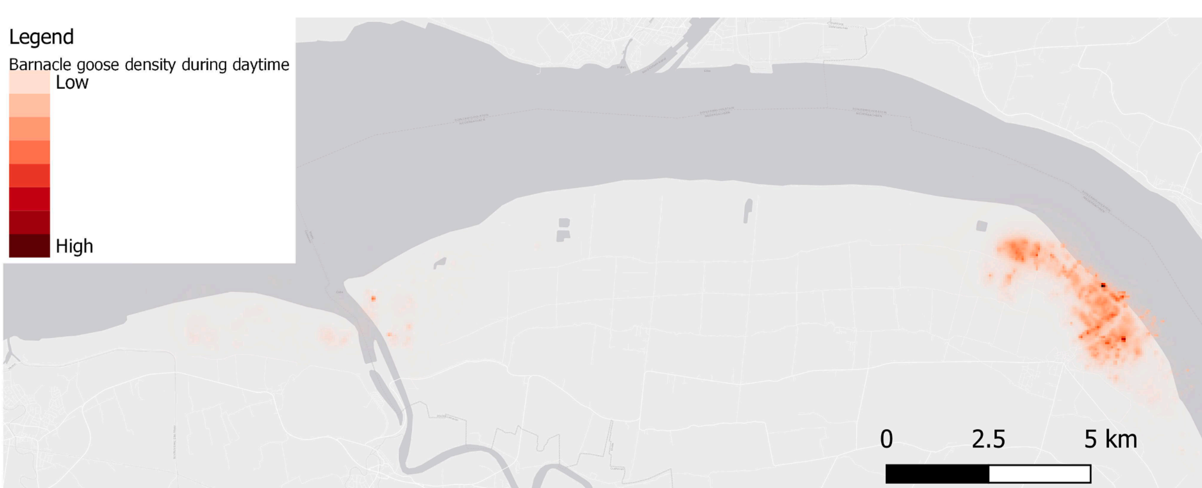

Fig. A1. Barnacle geese density during daytime within wader nesting season (1st April until 31st May) in the year 2016 based on GPS transmitter data with a ground speed of < 20 km per hour. A darker red colour indicates a higher density of barnacle geese. Created with dynamic Brownian Bridge Movement Model (function: "Brownian.bridge.dyn" in the R-package "move", window size = 31, margin = 13). (background map: ESRI, 2012)

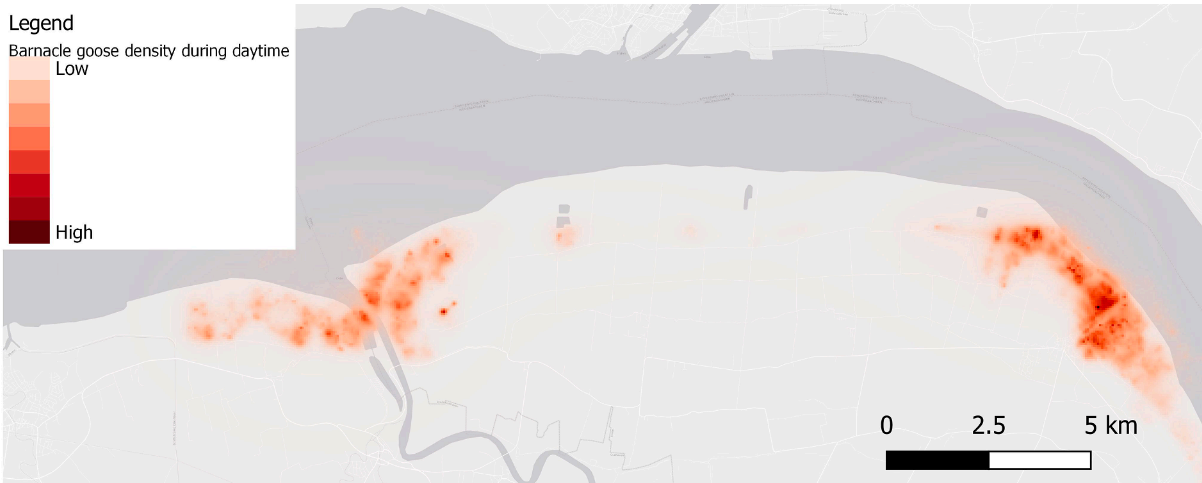

Fig. A2. Barnacle geese density during daytime within wader nesting season (1st April until 31st May) in the year 2017 based on GPS transmitter data with a ground speed of < 20 km per hour. A darker red colour indicates a higher density of barnacle geese. Created with dynamic Brownian Bridge Movement Model (function: "Brownian.bridge.dyn" in the R-package "move", window size = 31, margin = 13). (background map: ESRI, 2012)

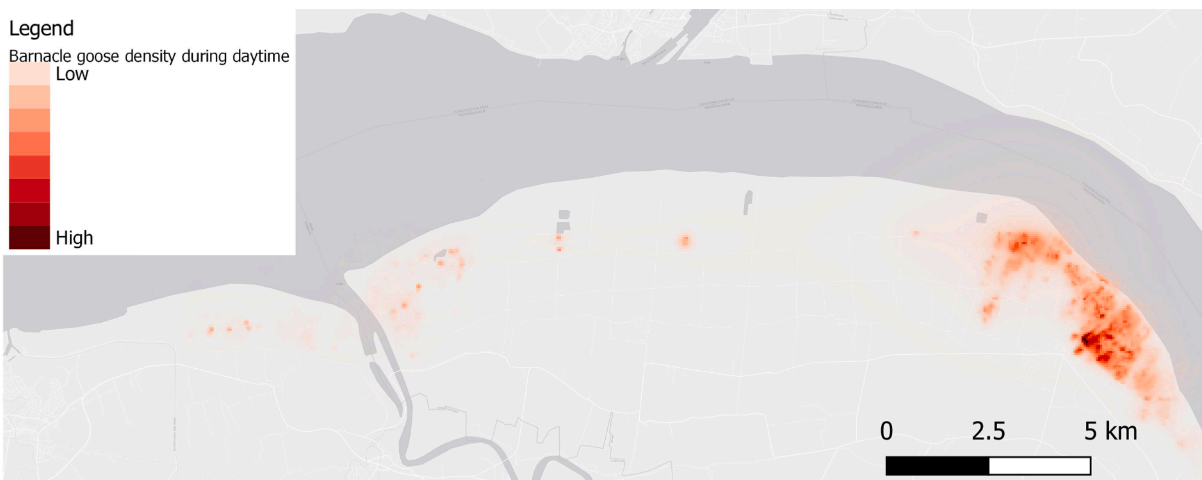

Fig. A3. Barnacle geese density during daytime within wader nesting season (1st April until 31st May) in the year 2018 based on GPS transmitter data with a ground speed of < 20 km per hour. A darker red colour indicates a higher density of barnacle geese. Created with dynamic Brownian Bridge Movement Model (function: "Brownian.bridge.dyn" in the R-package "move", window size = 31, margin = 13). (background map: ESRI, 2012)

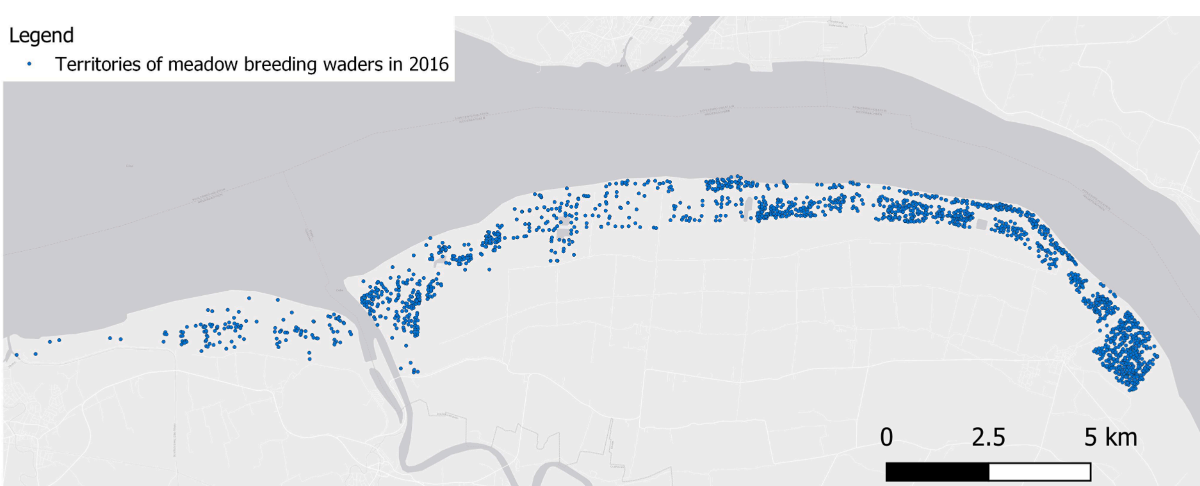

Fig. A4. Territories of meadow-breeding waders in the year 2016 (n = 1946) within the study area marked with blue dots. (background map: ESRI, 2012)

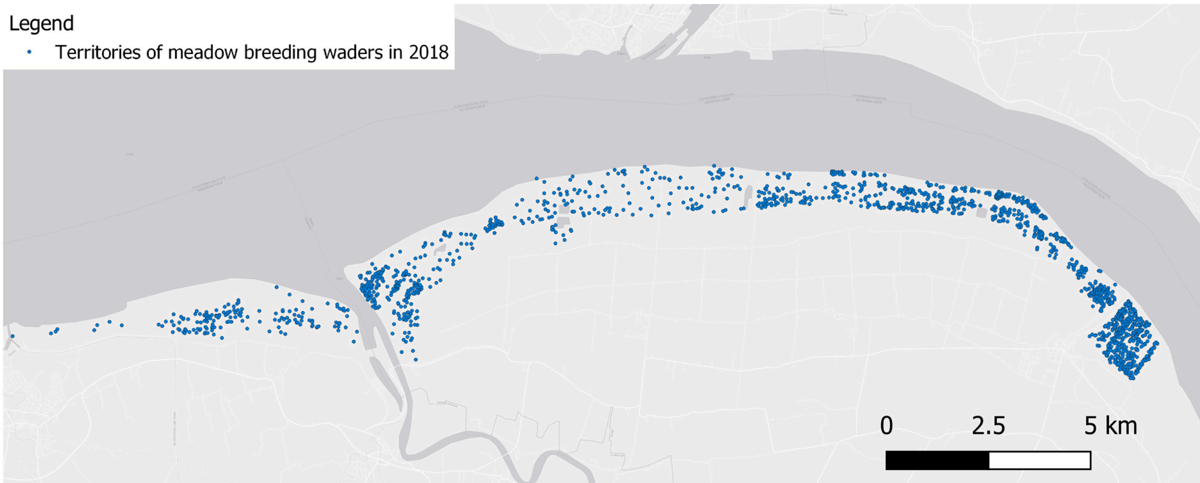

Fig. A5. Territories of meadow-breeding waders in the year 2018 (n = 1643) within the study area marked with blue dots. (background map: ESRI, 2012)

reason for the high densities, therefore we included nest density as a predictor in our analyses. It did however show no effect and is expected to be of less importance than other factors within the research area. Nest success rate of lapwings was negatively influenced by both barnacle goose density and the interaction between barnacle geese density and ground surface height. A possible explanation for the negative correlation between barnacle geese density and nest success of the lapwing, is that the lapwing is a very aggressive nest defender (Eriksson & Götmark, 1982). The lapwings could be spending a higher amount of time off the nest in its defence. However, the opposite was found by Kleijn and Bos (2010), who found that the nest incubation time increased when barnacle geese were active closer to a Lapwing nest. If this was the case in our study area as well, it could mean that the increased incubation time as a result of higher barnacle geese density resulted in increased temperature of the eggs which in other bird species resulted in lower hatching success (Nakage et al., 2003). Another explanation could be that the presence of barnacle geese attracts more predators towards an area, which might increase predation on wader nests. Lastly it might also be, that barnacle geese are more attracted to certain areas with either high or low moisture levels or other environmental factors that negatively affect the wader nest success which means that it is not a direct effect of barnacle presence. Despite the negative association between nest success of lapwings and the density of barnacle geese, the nesting density of lapwings was higher within our research area when compared to other areas in Lower Saxony.

4.3. Future research

Barnacle geese shortening sward height benefits wader territory selection (Vickery et al., 1997). Comparing sward heights and the diversity in sward height at nesting territories and random location, could help to explain the effect of sward height on territory distribution and authors of this research recommend to investigate this in future follow up studies. An experiment could be designed, where environmental variables are kept the same, and comparing areas with high density of barnacle geese with areas in which barnacle geese are excluded; however, this would be a challenge within a field situation and will likely only be possible in a caged environment. An important explanatory variable for some of the wader species in our study was waterlogging management; this was, however, a categorical variable investigated on a field scale. Measuring real continuous moisture levels on a smaller scale within both nesting territories and random territories could give more insight in the territory distribution of meadow-breeding waders.

To identify the underlying mechanism that caused the decrease of nest success with increased barnacle goose density further research is needed. During such a research lapwing breeding areas should be compared with and without the presence of barnacle geese, taking into account differences in time spend on vigilant and defensive behaviours. In addition, moisture/water levels should be measured as they are known to affect nesting success and barnacle goose presence. Maybe undesirable water levels for nest success might be the preferred area for barnacle geese causing them to show a negative correlation with lapwing nest success. Within such research also grass height should be measured as this is likely affected by barnacle geese and might cause reduced nest success.

4.4. Management implications

Although our models only explain part of the variation in the wader territory distribution, our results reveal that higher densities of barnacle geese do not negatively affect territory distribution of meadow-nesting waders. The current management of our study area is already focused on promoting growth and maintenance of meadow-breeding waders by low cattle grazing, no use of fertilizer or pesticides and perform waterlogging on a number of fields. In order to stimulate the growth of meadow-breeding wader populations, we advise increasing the number of fields on which waterlogging takes place, which attract species such as the lapwing, redshank, godwit and the ringed plover. From our results, we expect this will attract barnacle geese, which could reduce the number of geese foraging on grassland fields with agricultural purposes, reducing agricultural damage. Grazing geese will also benefit some wader species preferring lower sward heights, especially with the warming climate causing grass growth even during winter months. After all, large grazers such as cattle, are known to trample wader nests, especially with higher cattle densities (Mandema et al., 2013). Grazing by barnacle geese during winter months will maintain a low sward height, which will attract breeding waders during spring; in addition, barnacle geese are not known to trample wader nests. Further research on the effect of barnacle geese on nest success of wader species is needed to identify if the negative effect found within our research is really a direct effect of barnacle geese, so that this can be taken into account in future management plans. Nest protection experiments could give further insight as this might reduce the direct influence of foraging geese on waders.

5. Conclusion

After our research we can conclude that the investigated meadow breeding waders were not negatively influenced by barnacle geese density during their territory selection. Therefore, management of barnacle geese in high density areas is not needed in order to improve wader conservation during the phase of territory selection. Lapwing nest success seemed to be less in areas with higher barnacle geese densities. However, further research is needed to find out if these are direct effects of barnacle geese, or effects caused by environmental factors. These environmental factors could benefit both foraging barnacle geese and waders searching for territory, however they could cause a decrease of the nest success of lapwings. To adept management and conservations strategies to increase nest success of waders more research is needed towards the effects of barnacle geese and other geese species.

Author contributions

Gerard Müskens, Sander Moonen, Helmut Kruckenberg and Jürgen Ludwig performed geese catching and tagging. Jürgen Ludwig gathered data on territory distribution and nest success. Sander Moonen, Bart Nolet and Henk van der Jeugd designed data analyses. Sander Moonen performed analyses and wrote the article, and all other authors revised and improved the draft versions and gave final approval for publication.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: S. Moonen reports financial support was provided by Ministerium für Ernährung, Landwirtschaft und Verbraucherschutz. F. Bairlein reports financial support was provided by Ministerium für Ernährung, Landwirtschaft und Verbraucherschutz. H. Kruckenberg reports financial support was provided by Ministerium für Ernährung, Landwirtschaft und Verbraucherschutz. J. Ludwig reports financial support was provided by EU LIFE Nature.

Data availability

Data will be made available on request.

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Appendix

dBBMM model 2016
See Fig. A1.
dBBMM model 2017
See Fig. A2.
dBBMM model 2018
See Fig. A3.
Nest site distribution 2016
See Fig. A4.
Nest site distribution 2018
See Fig. A5.

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