Distribution of Barnacle Geese Branta leucopsis in Relation to Food Resources, Distance to Roosts, and the Location of Refuges

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We used GPS satellite tracking data and field measurements of vegetation to investigate the effect of food resources, distance to roosts, and the location of refuges on the distribution of Barnacle Geese *Branta leucopsis* in the northern part of The Netherlands. To deal with spatial dependence among the data, a spatial lag model was used. A significant quadratic effect was found between sward height and goose distribution, indicating that geese prefer patches with intermediate sward heights. The manipulation of sward height can therefore be used to attract geese to refuges and thus reduce goose grazing in agricultural land. No relationship was found between grass nitrogen content and grazing intensity, indicating that geese do not distinguish between areas based on nitrogen content. A higher grazing intensity was observed in areas located within 2 km from roosts. The eight tracked geese spent 80% of their foraging time in refuges, demonstrating the importance of the refuge system.

Key words: satellite tracking, goose grazing intensity, sward height, green biomass, nitrogen, distance to roosts, refuges, spatial lag model

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The distribution of avian herbivores is to a large extent influenced by food availability (Prins & Ydenberg 1985, Fryxell 1991). Animals spend more time in patches that enable them to have a higher intake of energy (de Boer & Prins 1989, Prins 1996, Raoguet *et al.* 1998) or nutrients (Ydenberg & Prins 1981, Durant *et al.* 2004, Bos *et al.* 2005). Small herbivores require a higher nutrient concentration in their diets than large herbivores, as they are less capable of utilizing poor quality plants (Prins & Ydenberg 1985, Durant *et al.* 2004, Prins & van Langevelde 2008). For instance, the Barnacle Goose *Branta leucopsis* requires food containing more than 15% crude protein to meet nitrogen requirements (Prop & Deerenberg 1991, Amano *et al.* 2004). Furthermore, waterfowl have food retention times as short as a few hours (Prop & Vulink 1992, McKay *et al.* 1994), which is reflected by a high throughput and defecation rate (Owen 1980). Such a digestive system requires a high ingestion rate and only allows for easily digestible components (Karasov 1990). To achieve this, avian herbivores select feeding sites of intermediate biomass, trading-off forage quality and quantity (Durant *et al.* 2004, Heuermann 2007). Foraging performance by herbivorous waterfowl has been well explored under

experimental conditions, in particular to understand decisions that take place at a small scale (Riddington *et al.* 1997, Hassall *et al.* 2001, Bos *et al.* 2004). However, processes that take place at the habitat scale have been investigated less often. This scaling-up could reveal important insights into the factors that determine grazing pressure by geese (Vickery & Gill 1999).

Populations of herbivorous waterfowl in the western Palaearctic have increased strongly over the last decades due to changes in land use and hunting regimes (Madsen *et al.* 1999). Conflict with agriculture has intensified because herbivorous waterfowl feed to a large extent on agricultural land (van Eerden *et al.* 2005). The establishment of a refuge system to accommodate these birds is regarded to be an effective, long-term solution to the problem (Owen 1977, 1980, McKay *et al.* 2001). In Europe, the highest densities of herbivorous waterfowl are found in The Netherlands, where the heavily fertilized agricultural lands provide attractive foraging areas (Prins & Ydenberg 1985, Madsen & Fox 1995, van Eerden *et al.* 2005). To alleviate problems, accommodation areas have been designated as refuges (Leistra *et al.* 2008), in addition to existing refuge areas (in semi-natural areas including salt marshes, fresh-water marshes, and some extensively managed grasslands). Refuges are generally located close to larger water bodies, as waterfowl are known to prefer foraging close to their roosts, to save travelling time and energy (Owen 1980, Owen *et al.* 1987, Vickery & Gill 1999). However, this distance effect may vary in time and among geographical areas. Waterfowl are also sensitive to human disturbance (Owen 1980, Hockin *et al.* 1992, Vickery & Gill 1999). It is therefore assumed that disturbance could stimulate birds to forage in designated refuges. Within these refuges, the influence of food resources and distance to roosts are expected to be more pronounced than in the surrounding non-refuge areas, where disturbance plays an important role.

This study aims to investigate how food resources, distance to roosts, and the location of refuges influence the distribution of Barnacle Geese during spring staging. Our results have implications for conservation and can be used to further improve wildfowl refuge management.

METHODS

Study area
Our study area was situated in the northern part of The Netherlands, in the provinces of Groningen and Friesland (Fig. 1). Field sampling of forage quality and quantity was carried out in the Lauwersmeer area (70% agricultural grasslands, 30% semi-natural grasslands). Agricultural lands are managed by farmers, with regular fertilization, mowing, and cattle grazing. Semi-natural areas are managed by different organizations as nature reserves, some of which allow year-round grazing by cattle. In accommodation areas, wildfowl were not allowed to be disturbed from 1 November to 1 April, while in nature reserves waterfowl are fully protected. A variety of scaring methods have been developed for non-refuge areas (e.g. gas canons, scarecrows, dog chasing). However, if chasing the geese does not result in reduced damage to agriculture, killing by shooting is permitted (killing Barnacle Geese is not allowed in this region). The plant community in agricultural fields is dominated by *Lolium perenne* and *Poa pratensis*. Low and middle height plant species (forage for herbivorous waterfowl) in semi-natural areas include *Festuca rubra*, *Puccinellia maritima*, *Agrostis stolonifera*, *Plantago maritima*, and *Triglochin maritima*.

Satellite tracking data of Barnacle Geese
In January 2008, eight adult Barnacle Geese were caught in the Lauwersmeer area and fitted with 30-g solar-powered GPS PTT transmitters (PTT 100 series, accuracy ±18m Microwave Telemetry, Inc., Columbia, MD, USA). The transmitters were fastened by Cordura-Nylon harness (for details see Ens *et al.* 2008). The transmitters recorded GPS locations four times per day (at 7:00, 10:00, 13:00, and 16:00 CET), and the collected data, including goose ID, date, time, longitude, latitude, speed, course and altitude, were transmitted every three days (for details see Ens *et al.* 2008). A total of 1468 GPS locations were recorded in the provinces of Friesland and Groningen from 1 February to 18 May in 2008, after which the tracked geese had left The Netherlands (Fig. 1). The temporal distribution of the recorded GPS locations is displayed in blocks of three days in Figure 2, indicating the continuity of records.

Previous studies indicate that geese forage during 70% of the daylight period in the spring (Prins *et al.* 1980, Black *et al.* 1991, van der Graaf 2006). We therefore assumed that from March to April, locations recorded were grazing locations. In order to exclude locations recorded during flight, GPS locations associated with a speed of more than 1 km/h were not used. GPS locations corresponding to the time of field sampling (March and April 2008), were imported into the ArcGIS software (www.esri.com) as point data ($n = 1025$). This point data layer depicted bird grazing at specific locations. To quantify the spatial distribution of
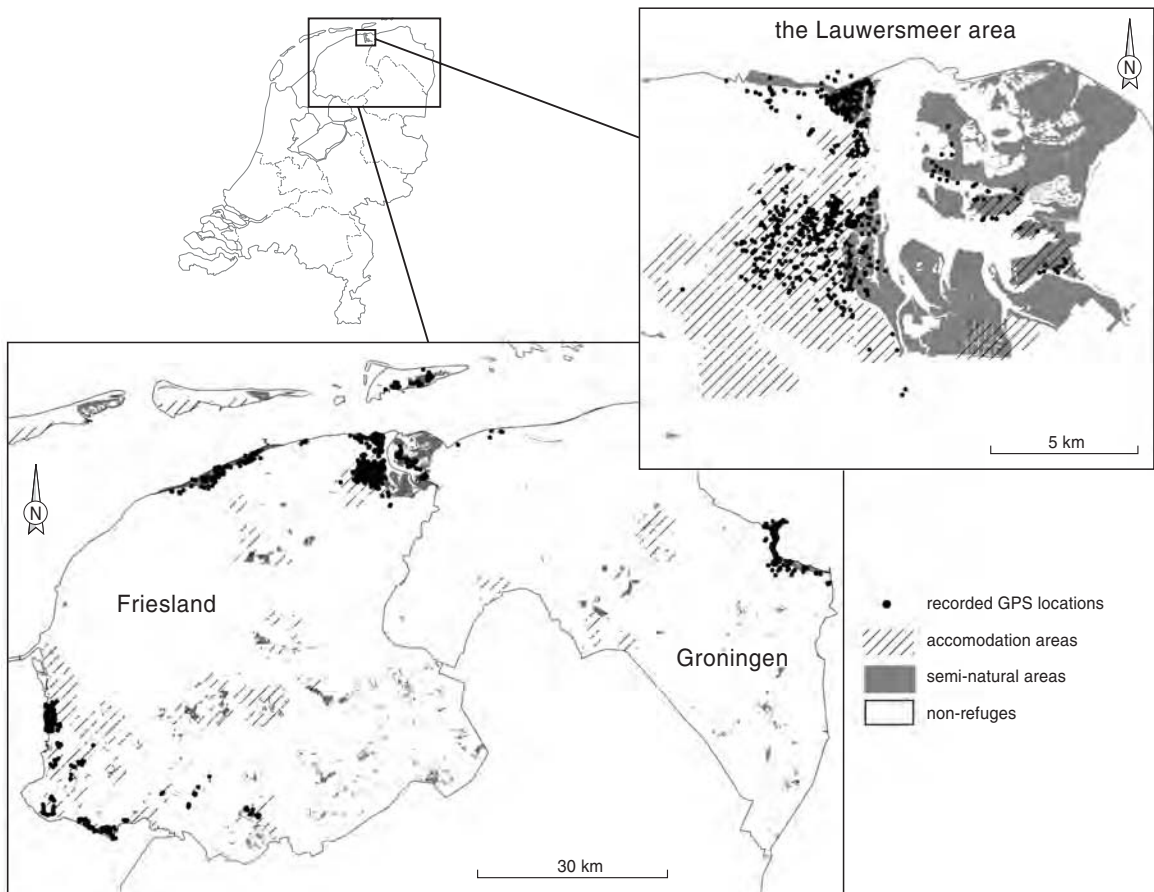
Figure 1. Spatial distribution of recorded GPS locations of eight Barnacle Geese in the provinces of Friesland and Groningen, The Netherlands. The records stem from 1 February to 18 May 2008, after which the geese migrated towards Russia. The locations of semi-natural areas were extracted from the Dutch National Landuse Database.
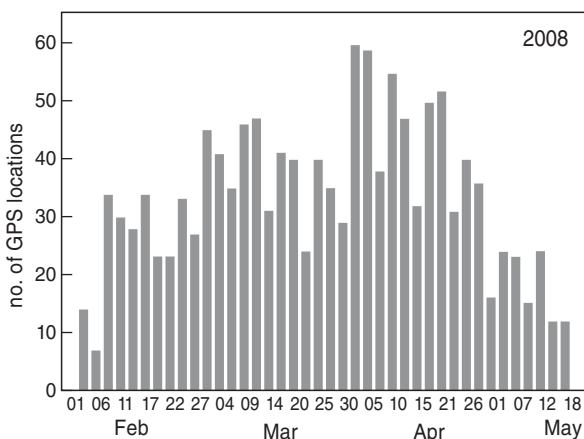

Figure 2. Temporal distribution of the recorded GPS locations of eight Barnacle Geese in the provinces of Friesland and Groningen, 1 February to 18 May 2008. The bars indicate the number of locations received every three days.

birds, a grazing intensity map (the number of recorded GPS locations of Barnacle Geese per km^2) was generated, using a fixed kernel density estimator with 95% space-use contours. This is a commonly applied space-use estimator in wildlife studies and has been used to estimate resource selection (Marzluff *et al.* 2004, Millspaugh *et al.* 2006). By overlaying the vegetation sample data on the generated density map, the grazing intensity for each vegetation sample was extracted. Vegetation samples located outside the 95% space-use contours were excluded from analysis, as grazing density data was not available in these areas. A total of 55 samples were retained for further analysis.

Field data collection

Fieldwork was conducted from 20 March to 13 April in 2008. We focused on spring because Barnacle Geese in winter mainly graze on heavily fertilized agricultural
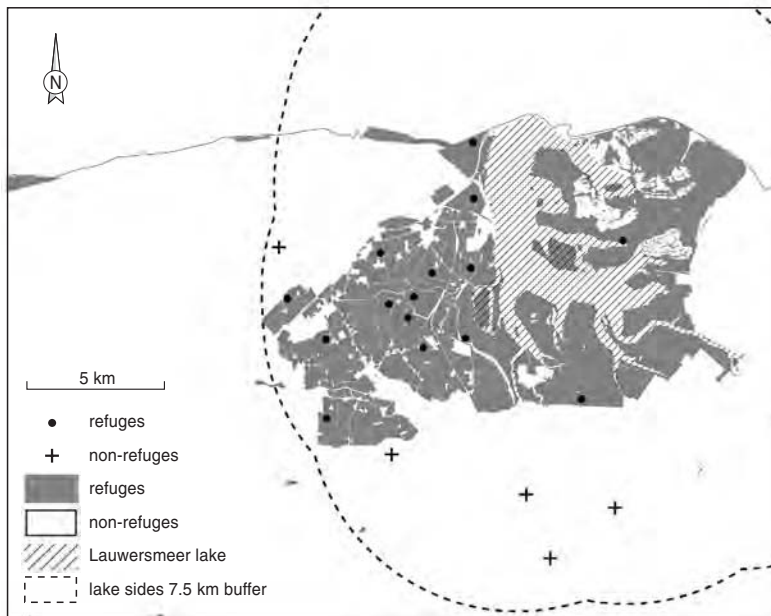
Figure 3. Distribution of twenty sampling locations in refuges and non-refuges in the Lauwersmeer area. All field locations were situated within a 7.5 km buffer from the lake sides.

land (Prins & Ydenberg 1985, van der Graaf 2006), whereas both agricultural and semi-natural areas are utilized during spring (Bos & Stahl 2003). The foraging areas of Barnacle Geese are up to 7.5 km from their roost sites (Owen *et al.* 1987, Vickery & Gill 1999). Therefore, for geese roosting on the Lauwersmeer lake, a 7.5 km buffer was generated from the lake sides to define the maximum extent of the potential feeding area. Non-refuge areas were defined as those areas situated within the perimeter of the 7.5 km buffer, but outside of accommodation areas, semi-natural areas and the Lauwersmeer lake (Fig. 3).

A stratified sampling design was adopted, based on two strata: refuges and non-refuges. The refuge areas were more intensively sampled than the non-refuges, because geese were mostly observed in refuges during the field survey. In total, 20 random locations were generated, with 15 located in refuges and 5 in non-refuges (Fig. 3). For each location, 5 random sample plots were generated within a square (300 × 300 m), resulting in 75 samples in refuges, and 25 samples in non-refuges. Additionally, the samples covered both agricultural (75) and semi-natural grasslands (25). We assumed that the grass conditions were relatively stable during the 3–4 week sampling period (either consistently or little/not grazed by geese).

Three vegetation variables were measured: green biomass, sward height and nitrogen concentration. Green biomass and sward height were used as forage quantity indicators, whereas nitrogen concentration was used as a measure of forage quality. Samples were taken from a plot of 1 × 1 m. Because of the homogeneity of the swards, we assumed that small sampling areas (0.1 × 0.1 m) adequately represented the biomass level of the bigger plots (1 × 1 m) (e.g. Owen 1971, Harwood 1977). The sampling area was clipped to ground level using hand shears and samples were stored in sealed plastic bags. In the lab, non-green parts were discarded and the remaining green portions were dried at 70°C for 48 h and subsequently weighed. Sward height was measured by pushing a ruler vertically through the sward until it came to rest on the soil surface (Stewart *et al.* 2001). By placing a carton disc on top of the vegetation, the sward height was read off the ruler. Sward height was recorded as a mean of ten random positions within each sample plot. Twenty leaf samples per plot were collected for nitrogen analysis by taking leaves between the forefinger and thumb, simulating goose grazing. Nitrogen concentration (%) was analyzed in the Resource Ecology Group laboratory of Wageningen University, using a SkalarSan-Plus auto analyzer, after destruction with a mixture of H_2SO_4, selenium and salicylic acid (Novozamsky *et al.* 1983).

Statistical analysis

We first tested how the distance to the nearest roost influenced grazing intensity. The number of recorded GPS locations was calculated within 7 distance buffers ranging from 1 to 7.5 km, with an increase of 1 km (the outermost buffer was from 6 to 7.5 km). A distance

threshold was identified to distinguish areas with high cumulative grazing intensity from low intensity, based on the number of recorded GPS locations in each distance buffer. Field samples were categorized into two groups: within and beyond the distance threshold. The difference in grazing intensity between these two groups was tested using a one-way ANOVA, with grazing intensity as a dependent variable and occurrence within or beyond the distance threshold as a fixed factor. Categorizing the field samples into two groups could relax the influence of the distance to roost on the grazing intensity of geese. The relationship between food conditions and grazing intensity would therefore be more pronounced in each subset than in the pooled data.

Geese prefer sites of higher forage quality when nitrogen is in limited supply, but do not distinguish when overall forage quality is sufficiently high. Previous studies found a positive relationship between food quality and goose grazing intensity for nitrogen concentration in green leaves below 2.4% (Prop & Deerenberg 1991), but above 3.2% (National Research Council 1994) no relationship was discovered. Meanwhile, geese prefer sites of intermediate forage quantity as their foraging efficiency drops at high sward height due to increased handling time (van de Koppel *et al.* 1996, van der Wal *et al.* 1998, Heuermann 2007). An ordinary partial least square (OLS) regression was fitted to test the effects of food resources and distance to roosts on grazing intensity. The predictive variables included nitrogen concentration, amount of green biomass, squared green biomass, sward height, squared sward height, and categorized distance to roosts. The OLS model assumes either the observations are independent or the residuals from the OLS estimation are uncorrelated (Haining 1990). The existence of spatial dependence will make the use of OLS regression questionable, as violation of these assumptions may result in biased and inefficient estimation of the parameters of the regression model. Therefore, a $N{\times}N$ spatial weights matrix W was generated to identify neighbouring fields for spatial diagnostics and spatial model estimation. The diagonal elements are zero. The off-diagonal elements, $W_{k,l}$, represent neighbour relations between observations k and l. A common method for choosing spatial weights is to use geographic criteria, such as points being within a critical distance (Anselin 2006). We used 300 m as the threshold value, based on the sampling scheme. We then executed Moran's I (Moran 1950) based on the spatial weights matrix to measure the degree of spatial dependence of the OLS model residuals. Moran's I is powerful in detecting misspecifications, but less helpful in suggesting alternative specifications. Two Lagrange Multiplier (LM) tests were therefore used to identify which of the two common spatial processes, spatial lag or spatial error, is the cause. The LM Lag test evaluates if the lagged dependent variable should be included in the model, and the LM Error test assesses if the lagged residual should be included. Robust versions of the statistics are considered only when the standard versions are significant. They can be conducted to verify if the spatial lag dependence is robust and therefore spatial error dependence can be ignored and vice versa.

Spatial dependence can be modelled by the spatial lag model or the spatial error model. In the spatial lag model, the value of a dependent variable Y at a location is modelled as a function of the independent variables X in that location as well as the values of the dependent variable at the neighbouring locations, i.e. the spatial lag. A spatial lag is the weighted average of the dependent variable values at the neighbouring locations (Anselin 2006), included as an additional explanatory variable in the model. The spatial error model addresses the spatial autocorrelation existing in the regression residuals of the OLS model. The value of the dependent variable Y in a location is redefined as a function of the independent variables X and the regression residuals of the neighbouring location, i.e. the spatial error. A spatial error is a weighted average of the individual residuals of the neighbouring locations, which is added into the model as an additional explanatory variable. The spatial lag model assumes that grazing intensity depends on the intensity observed in neighbouring fields and a set of environmental factors. The spatial lag model is theoretically consistent with the situation where grazing rate in one field is jointly determined with that of the neighbouring fields.

The Akaike Information Criterion (Akaike 1974) is a model selection criterion based on the distance between the estimates of the model and the true values, which allows models of different types to be compared directly. A smaller AIC value indicates better goodness of fit and therefore the model with the least AIC is regarded as the better model. AIC was used to compare OLS and spatial autoregressive models. Since the OLS models report goodness of fit using R^2, whereas the spatial autoregressive models use pseudo R^2, they are not directly comparable (Veall & Zimmermann 1996). The spatial dependence of the two model residuals was also compared using Moran's I scatterplots.

All recorded GPS locations ($n = 1468$) from 1 February to 18 May were utilized to compare the

frequency of goose visits in refuges and non-refuges. The numbers of locations recorded in refuges and non-refuges were calculated for each month. Thereafter we analysed data at the Lauwersmeer area in March and April 2008 and compared the forage conditions in refuges and non-refuges. All field data were tested for normality using a Kolmogorov–Smirnov test. Percentage data (nitrogen concentration) were arcsine-square root transformed (Zar 1999). To test whether the forage quality and quantity were different within and outside the refuges, a one-way ANOVA was used, with nitrogen concentration, green biomass and sward height as dependent variables, respectively, and location inside or outside refuges as a fixed factor. The forage conditions within and outside of refuges could be compared because the main plant species were similar (2/3 of the samples in refuges and all samples in non-refuges were collected from agricultural grassland).

RESULTS

Forage conditions and distance to roosts

The number of recorded GPS locations of Barnacle Geese in different distance buffers revealed a high cumulative grazing intensity in fields within 2 km from the roost, accounting for 83% of the total recorded locations (Fig. 4A). The field samples were therefore categorized into two groups: within and beyond 2 km from the nearest roost. A significantly higher grazing intensity was observed at sample locations within 2 km from the nearest roost than for locations beyond (Fig. 4B: $F_{1,53} = 22.03$, $P < 0.001$).

Following the basic fitting of the OLS model (Table 1), we estimated the value of Moran's I for the fitted model residuals. This is equivalent to testing the assumption of the OLS model that the residuals from the model fit are independent. The residuals of the
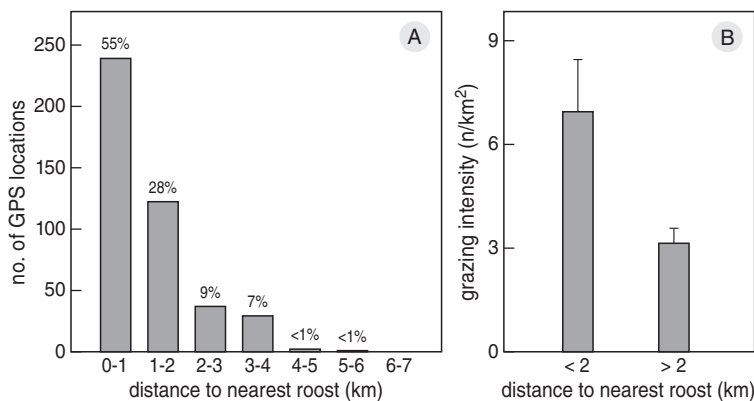
Figure 4. Numbers of recorded GPS locations of eight Barnacle Geese in different distance buffers (A) and the grazing intensity in field samples located within and beyond 2 km from the roost (B) in the Lauwersmeer area March and April 2008.

Table 1. Parameter estimates and statistics for the OLS and Spatial lag models for predicting goose grazing intensity from forage quantity, quality, and roost distance.

Model	OLS			Spatial lag		
R-squared	0.487			0.737		
Log-Likelihood	–129.1			–114.4		
AIC	272.3			244.9		
No. of observations	55			55		
Parameters	Coefficient	t-statistic	P	Coefficient	t-statistic	P
Sward height	4.537	3.21	0.002	4.331	4.58	<0.0005
Sward height^2	–0.516	–2.67	0.010	–0.480	–3.72	<0.0005
Green biomass	0.094	1.99	0.052	0.051	1.59	0.111
Green biomass^2	–0.001	–2.68	0.010	–0.001	–2.38	0.017
Nitrogen	0.135	0.37	0.716	–0.185	–0.75	0.455
Distance to roost	–4.571	–5.25	<0.0005	–2.987	–4.56	<0.0005
Spatial lag variable				0.697	8.68	<0.0005

Table 2. Diagnostics for spatial dependence using Lagrange Multiplier tests.

| Test	df	Value	P
Lagrange Multiplier (lag)	1	34.150	<0.0005
Robust LM (lag)	1	7.008	0.008
Lagrange Multiplier (error)	1	27.457	<0.0005
Robust LM (error)	1	0.315	0.575

OLS model presented a significant level of positive spatial autocorrelation, with a Moran's I value of 0.419 ($P < 0.001$). The presence of spatial dependence in the data violates the independence assumption of the OLS regression and demands explicit treatment with a spatial autoregressive model.

LM and LM Robust tests were performed in order to select between the spatial lag and spatial error models (Table 2). The LM Lag test and LM Error test both suggested significant spatial dependence. We therefore analysed the robust forms of the test. The Robust ML-Lag was significant ($P = 0.008$) while the Robust ML-Error was not ($P = 0.575$), indicating that the spatial lag specification was more appropriate.

AIC values indicated a better fit for the spatial lag model than the OLS model (Table 1). Grazing intensity showed a quadratic relationship with sward height, with most intense grazing at intermediate height. Similar relationships were observed for green biomass, though the first order effect was not significant. No significant relationship was found between nitrogen concentration and grazing intensity. Both distance to roost and the spatial lag variables showed significant effects. The Moran's I of the residuals was reduced from 0.419 (OLS) to 0.071 (spatial lag model).

Food conditions in refuges and non-refuges

The eight tracked geese spent on average 80% of their grazing time in refuges from February to May 2008 in The Netherlands (Fig. 5A), and 94% within the 7.5 km potential grazing buffer around the Lauwersmeer lake (Fig. 5B). The percentage of recorded GPS locations in refuges decreased at both scales during this period (Fig. 5). There was no significant difference in forage quality between refuges and non-refuges, but the green biomass and sward height in refuges were significantly lower than those in non-refuges (Table 3).
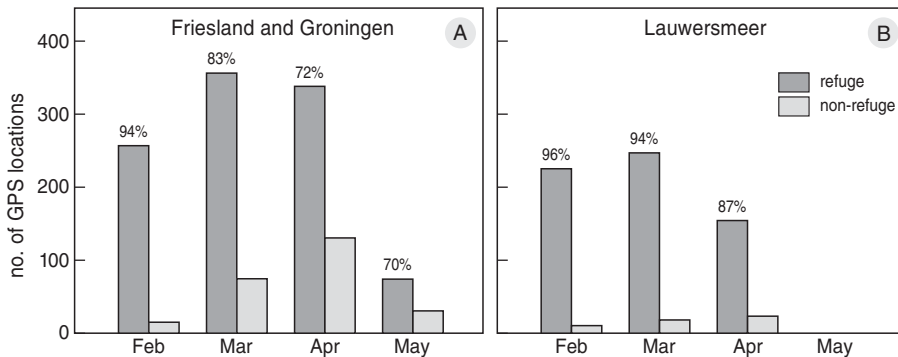
Figure 5. Monthly numbers of recorded GPS locations of eight Barnacle Geese in the provinces of Friesland and Groningen (A) and the Lauwersmeer area (B), from 1 February to 18 May 2008. The percentage of locations recorded in refuges for each month is shown above each bar.

Table 3. Food quality and quantity in and outside refuges in the Lauwersmeer area (The Netherlands).

	Field type	Mean	95% CI	n	$F_{1,98}$	P
Nitrogen (%)	Refuges	3.9	3.7–4.1	73	0.55[a]	0.462
	Non-refuges	4.1	3.8–4.4	25		
Green biomass (g DW/m^2)	Refuges	90.2	72.9–107.5	75	9.88	0.002
	Non-refuges	141.5	118.7–164.3	25		
Sward height (cm)	Refuges	4.0	3.0–4.9	75	5.94	0.017
	Non-refuges	6.1	5.2–6.9	25		

[a] $F_{1,96}$; calculated using transformed data.

DISCUSSION

Although our observations were based on a sample size as small as eight tagged birds, the study demonstrated clearly that amount of food, distance to roosts, and the location of refuges affected the distribution of spring staging Barnacle Geese. Food quality did not seem to affect goose distribution. Indeed, the sites selected by geese were of sufficiently high forage quality (nitrogen concentrations from 2.6% to 5.5%), which was well beyond the limit for Barnacle Geese of 2.4% (Prop & Deerenberg 1991, Amano *et al.* 2004). This lack of food quality effect is different from previous field experimental studies (Bos *et al.* 2005, van der Graaf *et al.* 2007), which demonstrated that fertilized plots were preferred above control plots. A possible reason is that for the experimental studies, switching between plots requires a negligible amount of energy to be spent on travelling, whereas, at the habitat level, the energy saving benefit of minimising the distance to roosts might overrule any food quality effect.

The observed dome-shaped relationship between sward height and grazing intensity reveals that an intermediate sward height is preferred by Barnacle Geese. Our findings emphasize the importance of sward height in determining the distribution of geese at the habitat level. Sward height manipulation can thus be an important tool in luring geese to refuge areas, thereby reducing grazing of vulnerable crops (Vickery & Gill 1999).

Distance to the nearest roost significantly influenced grazing intensity. Areas located within 2 km from the roost were preferred by geese over areas located beyond 2 km, and geese seldom used areas located more than 4 km from roosts. This finding is comparable with observations in the United Kingdom, where Barnacle Geese were found to feed within an average distance of 3.6 km from roosts (Owen *et al.* 1987).

The eight tracked geese utilized refuges much more intensively than non-refuges, indicating the importance of refuges. Methods to scare geese developed for non-refuge areas may play a prominent role in chasing birds away. Forage conditions in non-refuges, however, also decreased the usability of these areas for geese, due to tall swards. The mean sward height was 6 cm in non-refuges while the optimal sward height for birds the size of Barnacle Geese is 3 cm (Heuermann 2007). From February to May, utilization of refuges decreased, possibly because food became depleted, forcing geese to use non-refuge areas.

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REFERENCES

Akaike H. 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control. 19: 716–723

Amano T., Ushiyama K., Fujita G. & Higuchi H. 2004. Alleviating grazing damage by white-fronted geese: an optimal foraging approach. J. Appl. Ecol. 41: 675–688.

Anselin L. 2006. Spatial econometrics: methods and models. Kluwer, Dordrecht.

Black J.M., Deerenberg C. & Owen M. 1991. Foraging behaviour and site selection of barnacle geese *Branta leucopsis* in a traditional and newly colonised spring staging habitat. Ardea 79: 349–358.

Bos D., Drent R.H., Rubinigg M. & Stahl J. 2005. The relative importance of food biomass and quality for patch and habitat choice in Brent Geese *Branta bernicla*. Ardea 93: 6–16.

Bos D. & Stahl J. 2003. Creating new foraging opportunities for dark-bellied brent *Branta bernicla* and barnacle geese *Branta leucopsis* in spring – insights from a large-scale experiment. Ardea 91: 153–166.

Bos D., van de Koppel J. & Weissing F.J. 2004. Dark-bellied brent geese aggregate to cope with increased levels of primary production. Oikos 107: 485–496.

de Boer W.F. & Prins H.H.T. 1989. Decisions of cattle herdsmen in Burkina Faso and optimal foraging models. Hum. Ecol. 17: 445–464.

Durant D., Fritz H. & Duncan P. 2004. Feeding patch selection by herbivorous Anatidae: the influence of body size, and of plant quantity and quality. J. Avian Biol. 35: 144–152.

Ens B.J., Bairlein F., Camphuysen C.J., de Boer P., Exo K.-M., Gallego N., Hoye B., Klaassen R., Oosterbeek K., Shamoun-Baranes J., van der Jeugd H. & van Gasteren H. 2008. Tracking of individual birds: Report on WP 3230 (bird track-

ing sensor characterazation) and WP 4130 (sensor adaptation and calabration for bird tracking system) of the FlySafe basic activities. SOVON-2008/10. SOVON, Beek-Ubbergen.

Fryxell J.M. 1991. Forage quality and aggregation by large herbivores. Am. Nat. 138: 478–498.

Haining R. 1990. Spatial data analysis in the social and environmental sciences. Cambridge University Press, Cambridge, U.K.

Harwood J. 1977. Summer feeding ecology of lesser snow geese. J. Wildl. Manage. 41: 48–55.

Hassall M., Riddington R. & Helden A. 2001. Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. Oecologia 127: 97–104.

Heuermann N. 2007. Tall swards and small grazers: competition, facilitation and coexistence of different-sized grazers. PhD thesis, Wageningen University.

Hockin D., Ounsted M., Gormant M., Hillt D., Kellert V. & Barker M.A. 1992. Examination of the effects of disturbance on birds with reference to its importance in ecological assessments. J. Environ. Manage. 36: 253–286.

Karasov W.H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. Stud. Avian Biol. 13: 391–415.

Leistra G., Keulartz J. & Engelen E. 2008. Wintering geese in the Netherlands. In: Keulartz J. & Leistra G. (eds) Legitimacy in European nature conservation policy. Springer.

Madsen J., Cracknell G. & Fox, T. 1999. Goose populations of the western Palaearctic: a review of status and distribution. Wetlands International Publication 48, Wageningen.

Madsen J. & Fox A.D. 1995. Impacts of hunting disturbance on waterbirds – a review. Wildlife Biol. 4: 193–207.

Marzluff J.M., Millspaugh J.J., Hurvitz P. & Handcock M.S. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85: 1411–1427.

McKay H.V., Bishop J.D. & Ennis D.C. 1994. The possible importance of nutritional requirements for dark-bellied brent geese in the seasonal shift from winter cereals to pasture. Ardea 82: 123–132.

McKay H.V., Milsom T.P., Feare C.J., Ennis D.C., O'Connell D.P. & Haskell D.J. 2001. Selection of forage species and the creation of alternative feeding areas for dark-bellied brent geese *Branta bernicla bernicla* in southern UK coastal areas. Agricult. Ecosys. Environ. 84: 99–113.

Millspaugh J.J., Nielson R.M., McDonald L., Marzluff J.M., Gitzen R.A., Rittenhouse C.D., Hubbard M.W. & Sheriff S.L. 2006. Analysis of resource selection using utilization distributions. J. Wildl. Manage. 70: 384–395.

Moran P.A.P. 1950. Notes on continuous stochastic phenomena. Biometrika 37: 17–23.

National Research Council 1994. Nutrient requirement of geese. Nutrient requirement of poultry. National Academic Science (U.S.).

Novozamsky I., Houba V.J.G., Vaneck R. & Vanvark W. 1983. A novel digestion technique for multi-element plant analysis. Comm. Soil Sci. Plant Anal. 14: 239–248.

Owen M. 1971. The selection of feeding site by white-fronted geese in winter. J. Appl. Ecol. 8: 905–917.

Owen M. 1977. The role of wildfowl refuges on agricultural land in lessening the conflict between farmers and geese in Britain. Biol. Conserv. 11: 209–222.

Owen M. 1980. Wild geese of the world. Batsford, London.

Owen M., Black J.M., Agger M.K. & Campbell C.R.G. 1987. The use of the Solway Firth, Britain, by barnacle geese *Branta leucopsis* Bechst. in relation to refuge establishment and increases in numbers. Biol. Conserv. 39: 63–81.

Prins H.H.T. 1996. Ecology and behaviour of the African buffalo: social inequality and decision making. Chapman & Hall, London.

Prins H.H.T. & van Langevelde F. 2008. Assembling a diet from different places. In Prins H.H.T. & van Langevelde F. (eds) Resource ecology: spatial and temporal dynamics of foraging. Springer, Dordrecht.

Prins H.H.T. & Ydenberg R.C. 1985. Vegetation growth and a seasonal habitat shift of the barnachle goose (*Branta leucopsis*). Oecologia 66: 122–125.

Prins H.H.T., Ydenberg R.C. & Drent R.H. 1980. The interaction of brent geese (*Branta bernicla*) and sea plantain (*Plantago maritima*) during spring staging: field observations and experiments. Acta. Bot. Neerl. 29: 585–596.

Prop J. & Deerenberg C. 1991. Spring staging in brent geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. Oecologia 87: 19–28.

Prop J. & Vulink T. 1992. Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. Funct. Ecol. 6: 180–189.

Raoguet C., Dumont, B. & Prache S. 1998. Selection and use of feeding sites and feeding stations by herbivores: a review. Ann. Zootech. 47: 225–244.

Riddington R., Hassall b.M. & Lane S.J. 1997. The selection of grass swards by brent geese *Branta b. bernicla*: interactions between food quality and quantity. Biol. Conserv. 81: 153–160.

Stewart K.E.J., Bourn N.A.D. & Thomas J.A. 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. J. Appl. Ecol. 38: 1148–1154.

van de Koppel J., Huisman J., van der Wal R. & Olff H. 1996. Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. Ecology 77: 736–745.

van der Graaf A.J. 2006. Geese on a greene wave: flexible migrants in a changing world. PhD thesis, University of Groningen

van der Graaf A.J., Stahl J., Veen G.F., Havinga R.M. & Drent R.H. 2007. Patch choice of avian herbivores along a migration trajectory – from temperate to Arctic. Basic Appl. Ecol. 8: 354–363.

van der Wal R., van de Koppel J. & Sagel M. 1998. On the relation between herbivore foraging efficiency and plant standing crop: an experiment with barnacle geese. Oikos 82: 123–130.

van Eerden M.R., Drent R.H., Stahl J. & Bakker J.P. 2005. Connecting seas: western Palaearctic continental flyway for water birds in the perspective of changing land use and climate. Global Change Biol. 11: 894–908.

Veall M.R. & Zimmermann F.K. 1996. Pseudo R^2 measure for some common limited dependent variable models. J. Econ. Surv. 10: 241–59.

Vickery J.A. & Gill J.A. 1999. Managing grassland for wild geese in Britain: a review. Biol. Conserv. 89: 93–106.

Ydenberg R.C. & Prins H.H.T. 1981. Spring grazing and the manipulation of food quality by barnacle geese. J. Appl. Ecol. 18: 443–453.

Zar J.H. 1999. Biostatistical analysis. Prentice Hall, Englewood Cliffs.

SAMENVATTING

In de winter van 2008 werden acht Brandganzen *Branta leucopsis* bij het Lauwersmeer voorzien van een satellietzender. Dit bood de mogelijkheid te zien waar de vogels zich van dag op dag ophielden tot ze in de loop van april en mei naar het noordoosten wegtrokken. De gebiedskeuze in de noordelijke provincies kwam goed overeen met het al bekende verspreidingspatroon van de Brandgans met concentraties in het Lauwersmeergebied, langs de Wadden- en IJsselmeerkust van Friesland, op Schiermonnikoog en in de Dollard. Meer gedetailleerd onderzoek in het Lauwersmeergebied liet zien dat de acht ganzen de meeste tijd doorbrachten in delen die door de overheid voor ganzenopvang waren aangewezen ("foerageergebieden"). De ganzen foerageerden bij voorkeur binnen een straal van 2 km van de slaapplaatsen in het Lauwersmeer. Daarbuiten werd minder dan 17% van de tijd doorgebracht. De gebiedskeuze van de ganzen was afhankelijk van de lengte van het gras; gras met een lengte van 3–6 cm werd geprefereerd boven korter of langer gras. De kwaliteit van het gras (bepaald aan de hand van het eiwitgehalte) bleek niet van invloed te zijn op de gebiedskeuze. Kennelijk voldeed het eiwitgehalte overal aan de behoeftes van de ganzen.   (JP)