**A large-scale multi-species spatial depletion model for overwintering
waterfowl**

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Abstract

In this paper, we develop a model to evaluate the capacity of accommodation areas for overwintering waterfowl, at a large spatial scale. Each day geese are distributed over roosting sites. Based on the energy minimization principle, the birds daily decide which surrounding fields to exploit within the reserve boundaries. Energy expenditure depends on distance to the roost and weather conditions. Food intake rate is determined by functional responses, and declines with consumption. A shortage occurs when birds cannot fulfil their daily energy requirement. Most foraging takes place on pasture, with complementary feeding for some of the species on cereals and harvest remains. We applied the model to five waterfowl species overwintering in the Netherlands. From a comparison with field data, the model appears to produce realistic grazing pressures on pasture, especially for geese, and a realistic decline in sward height, but the use of arable fields is less in agreement with observations. For current goose and widgeon numbers, hardly any shortages are expected, but extrapolating the population increase observed during the last decade, considerable shortages are expected in the near future (2015). However, we find that several uncertainties may contribute to more severe shortages: a probabilistic (and therefore less optimal) choice of foraging location, a shorter maximum distance to the roost, and a lower effective availability of resources due to disturbances and other edge effects. Between species we find both competition and facilitation. Both type of interactions, as well as the spatial pattern of resource exploitation, are explained from functional responses and energetic costs of the species.

Key-words: central-place foraging, crop damage control, energy minimization principle, wildlife management, functional response on sward height, grazing waterfowl

1. Introduction

In flood plains and river deltas conflicts between man and wildlife are common. Both gather in these places to make use of the rich resources, with wildlife exploiting the very resources man is producing as food for itself or for its domestic animals. When involving species that are considered as pests by some but as conservation assets by others, wildlife management becomes contentious, as for instance in the case of goose management (Greenwood, 1993). Several attempts have been made to alleviate this conflict, which can be subdivided into goose population control (e.g., Hauser et al., 2007), compensation payments to farmers for crop damage inflicted by geese (van Eerden, 1990), and designation of reserves where geese are free to roam while they are chased away from other areas (Vickery and Gill, 1999). This paper deals with this third approach.

Obviously, a set-aside approach can only be effective when the size needed for the reserve can be reliably assessed. Reserve design is often based on island biogeography (MacArthur and Wilson, 1967) or metapopulation theory (Hanski and Ovaskainen, 2000). In territorial animals, the required reserve size can be derived from the minimum viable population size (in terms of breeding females) (Shaffer, 1981) and the minimum sustainable territory size (Nolet and Rosell, 1994). Similarly, for wintering geese, the carrying capacity of a reserve is determined by the amount of available food resources, e.g. the area of grassland and/or of cropland with harvest remains. An additional aspect to take into account, however, is that geese behave as central-place foragers, spending the night on water and flying to surrounding land to forage during the day. Therefore, feeding areas can only be effective if they are located near roosts (Vickery and Gill, 1999). Roosts are often shared by several species, potentially leading to resource competition in the fields around the roost.

According to the ideal free distribution, birds will always go to the habitat with the highest suitability (Fretwell and Lucas, 1970). As more and more birds enter the most suitable habitat, suitability is assumed to decline until being equal to that of the second best habitat, after which birds will start using both habitats, etc. The mechanism by which suitability declines can be interference (Goss-Custard et al., 1995), but also food depletion (Sutherland and Anderson, 1993). Up to now, depletion models have mainly been used for retrodicting bird numbers at small spatial scales (Sutherland and Allport, 1994; Percival et al., 1996; Nolet et al., 2006), but at least one attempt has been made to apply this framework at a nation-wide scale (Gill et al., 2001). This latter study has however been criticized for using observed lowest giving-up densities as the threshold food density at which predators are in energy balance (Van Gils et al., 2004). Here we develop a depletion model that can be applied at a large spatial scale where the giving-up density is an output rather than an input variable. As the basis of our model we use the energy minimization principle, which has been shown to apply in a wintering bird (Masman et al., 1988). Through this principle, a straightforward link between the birds' objectives and food depletion is made. The model takes into account the distribution of four types of food sources and the (observed) numbers and distribution pattern during the winter months of five goose or duck species. The model is spatially explicit, grid-based, and dynamic, and the five species involved affect each other directly and indirectly by exploiting the same food sources. Using an energy budget approach, assuming energy minimization, and taking into account daily weather conditions, we calculate where and when food shortages occur if the birds are restricted to foraging within reserve boundaries.

2. Material and Methods

2.1. Model overview

We developed a general model for spatial foraging of geese and ducks, and parameterized it for four geese and one duck species (wigeon). Actual choice of species was motivated by a case-study in which the model was applied (see 2.4). Food sources were grasslands, split into improved and semi-natural grassland, harvest remains (potatoes and beets) and wintergreens (cereals). Geese forage during the day on fields and rest during the night at water bodies. In contrast, wigeon mainly forage during the night and rest during the day (Brunckhorst, 1996).

The model landscape is defined spatially as a grid with square km cell-size. Resources are quantified by surface area and biomass density per cell within designated accommodation areas. Roosting sites are point-locations. Accommodation areas and roosting sites can be linked to geographic regions (e.g. provinces) to facilitate the use of bird census data and to provide output at the level of regions.

The model covers the winter period. It starts with an initial spatial distribution of resources in accommodation areas, and as further input, birds are distributed over roosting sites on a daily basis. Each day, for each roosting site, each species and each resource type, maps are generated with the distribution of the daily energy costs when feeding on parcels around the roost (Fig. 1). A parcel is defined as a single resource within a grid cell. Based on the energy minimization principle, the species' roosting site population will then fly to and forage on the parcel where they can attain energy balance at minimum daily energy cost (Masman et al., 1988). This parcel choice implies a trade-off between flight costs (to and from the parcel) and the attainable energy intake rate (at the

parcel) (van Gils et al., 2006; Van Gils and Tijssen, 2007). It also implies perfect knowledge by the birds where the best parcels are located around the roost, though this assumption can be relaxed by applying a probabilistic version of the model.

Resource density on the parcel will decrease with the amount consumed by the birds. When the selected parcel cannot support the whole roosting site population (e.g. when resource level is low, the population is too large, or as a result of competition from other roosting site populations or other species having selected the same parcel), the unsupported part of the roosting site population is directed to the parcel with the next lowest energy cost. Within the daily time step, this process of assigning foraging parcels continues until either the whole roosting site population is accommodated or not enough resource is available. In the latter case a shortage (or deficit) is recorded in terms of the percentage of birds unable to fulfil their daily energy requirement within the accommodation areas.

In order to prevent unrealistically high densities of birds at a parcel, we set a maximum density of 0.0075 birds m⁻² for improved grassland and wintergreens, 0.0050 m⁻² for semi-natural grassland (Bos, 2002), and $(2,000/(14 \times 10,000)) = 0.0140$ m⁻² for harvest remains (Gill et al., 1996). This maximum density includes all individuals irrespective of species, so summed over all species present at the parcel. If more birds are present than this maximum, then of each species only a fraction equal to the ratio of maximum density to total density can actually forage on the parcel, and the rest is reallocated to the second best parcel, etc.

We recorded number of birds successfully feeding on a resource, per species, roost, resource and grid cell, and from these calculated their numbers aggregated per period (month or whole winter) or region. Every individual bird unable to fulfil its daily energy requirement on a given day was

counted as a shortage of 1 bird-day. Daily shortages were calculated per species per roost. Resource depletion was made visible by keeping track of the resource biomass density (g m^{-2}) in each grid cell, per resource. Consequences of depletion, i.e. the need to forage at larger travelling distances from the roost, were estimated by keeping track of the distribution of foraging distances of all successful birds.

2.2. Energetics

We assume that the birds aim to be in energy balance, meaning that on a daily basis metabolizable energy intake (MEI , J d^{-1}) is equal to energy expenditure (DEE , J d^{-1}) (while, because of the energy minimization principle, DEE is minimal). A 24h day ($T = 86,400 \text{ s d}^{-1}$) is split into resting, flying (T_v , s d^{-1} , from and to a roost) and foraging time (T_f , s d^{-1}).

The daily intake of metabolizable energy (MEI , J d^{-1}) is the product of the instantaneous intake rate IIR (g s^{-1}), after conversion to metabolizable energy ($q \cdot e \cdot IIR$, J s^{-1}), and the daily foraging time T_f :

$$(1) \quad MEI = q \cdot e \cdot IIR \cdot T_f$$

where q is the assimilation and e (J g^{-1}) the energy content of the food. T_f is a function of the energy balance (see below).

The daily energy expenditure (DEE , J d^{-1}) is:

$$(2) \quad DEE = (T - T_f - T_v)RMR + T_f \cdot FMR + T_v \cdot VMR$$

where RMR ($J s^{-1}$) is resting metabolic rate, FMR ($J s^{-1}$) is field metabolic rate depending on weather (section 2.5.2), and VMR ($J s^{-1}$) is flying metabolic rate. Here, RMR is $1.4 \times BMR$ (basal metabolic rate), and FMR within the thermoneutral zone is $1.9 \times BMR$ (Stahl et al., 2001)

Flying is an energy-demanding activity. Flight time T_v ($s d^{-1}$) is $2V/v$ where V is the distance (m) from roost to the foraging parcel and v is the flight speed ($m s^{-1}$) (Clausen et al., 2002). The flight costs VMR ($J s^{-1}$) are allometrically scaled to body mass and wing span according to empirical data from other bird species (Norberg, 1996; Clausen et al., 2002). For parameter values per species see Table 1.

The bird is in balance when the time spent foraging yields a *net* intake of foraging exactly covering the costs of resting and flying. Equalling MEI to DEE , the required time spent foraging amounts to

$$(3) \quad T_f^* = \frac{(T - T_v)RMR + T_v \cdot VMR}{q \cdot e \cdot IIR - (FMR - RMR)}.$$

However, because the geese only forage during the day (and wigeon only during the night), the foraging time is limited by T_l , the available time (day length for geese and 24 h minus day length for wigeon). Hence, the available time can be shorter than the required T_f^* and thus the bird cannot cover its energy requirements on this particular parcel. Day length was calculated from the local daily meteorological data.

Through the principle of energy balance, energy expenditure can be regarded as a function of energy intake. After rearranging the formula of DEE :

$$(4) \quad DEE = T_f^* (FMR - RMR) + (T - T_v)RMR + T_v \cdot VMR$$

and substitution of T_f^* we obtain:

$$(5) \quad DEE = \frac{(T - T_v)RMR + T_v \cdot VMR}{q.e.IIR - (FMR - RMR)} (FMR - RMR) + (T - T_v)RMR + T_v \cdot VMR$$

Of course, the birds are assumed only to go foraging if this eventually yields *net* energy: $q.e.IIR - (FMR - RMR) > 0$. For all foraging parcels within the maximum distance (V_{max} , see Table 1) to a roosting site, species- and resource-specific values of DEE are calculated.

During cold weather with wind and little radiation from the sun, the costs of maintaining body temperature can be higher than the standard field metabolic rate FMR_S . Therefore, using the theory on heat exchange, we calculate the metabolic rate TMR needed to keep a bird body at 40 °C (Robinson et al., 1976; Cartar and Morrison, 1997; van der Graaf et al., 2001). If $TMR > FMR_S$, the realized field metabolic rate FMR is set to TMR , thus $FMR = \max(TMR, FMR_S)$. TMR is a function of ambient air temperature T_a (°C), wind speed u_{hc} (m s⁻¹) at $h_c = 10$ m, and the global radiation R_g (W m⁻²). The effect of cooling by wind is a function of the sward height. We neglect the heat loss through evaporation (Cartar and Morrison, 1997). For further details see Appendix.

2.3. Intake

On grassland and wintergreens, bite size S (g; all biomass in dry weight) is a function of sward height L (m) (Durant et al., 2003; Van Gils et al., 2007):

$$(6) \quad S_{(L)} = \frac{b_1 L}{1 + b_2 L}$$

where b_1 and b_2 are regression-coefficients. As these herbivores are foraging on spatially concentrated plants (process 3, Spalinger and Hobbs, 1992), total handling time T_h (s) is:

$$(7) \quad T_{h(S)} = T_c + \frac{1}{R_{\max}} S$$

where T_c is cropping time (s) and $R_{\max}$ the maximum rate of chewing (in the absence of cropping, $g s^{-1}$). The cropping time T_c is in turn a function of sward height L , presumably because the birds are becoming more selective with increasing sward height (Durant et al., 2003):

$$(8) \quad T_{c(L)} = T_{c0} + cL \quad (\text{Box 1, Heuermann, 2007}).$$

One should also consider that geese and wigeon regularly look up during foraging in order to check their surroundings. The ratio alert : feeding varies between 0.22 to 0.03, being lower the larger the group size (Spilling et al., 1999) and the shorter the day length (Ely et al., 1999). During alert the heart beat is elevated above resting levels (Nolet et al., 2002; Ackerman et al., 2004), and therefore we modelled alert as part of foraging. The intake rate is calculated over the time span feeding + alert, assuming a minimum proportion alert of 0.05. These processes together result in a type 4 functional response, with an instantaneous intake rate IIR ($g s^{-1}$) as function of sward height L :

$$(9) \quad IIR_{(L)} = \frac{S_{(L)}}{\alpha T_{h(S)}} = \frac{1}{\alpha} \left\{ \frac{1 + b_2 L}{b_1 L} (T_{c0} + cL) + \frac{1}{R_{\max}} \right\}^{-1}$$

where α is the factor with which the feeding time is multiplied to account for the alert time ($\alpha = 1.05$) (Fig. 2). See again Table 1 for parameter values per species.

The intake per bird (g d^{-1}) is:

$$(10) \quad I = IIR \cdot T_f$$

On harvest remains with density D (g m^{-2}) the instantaneous intake rate IIR (g s^{-1}) is modelled as a type 1 functional response:

$$(11) \quad IIR = a \cdot D$$

where attack rate a is scaled to that of Bewick's swans *Cygnus c. bewickii* Yarrell - the only species for which good estimates of intake rate are available (Nolet et al., 2002) – with a mass-exponent of 0.71 (Van Gils et al., 2007). The intake rate of Bewick's swans is $462 \text{ J s}^{-1} = 0.035 \text{ g s}^{-1}$, assuming a dry matter content of 0.15 g g^{-1} (Claassen, 1997), at a biomass of 16.4 g m^{-2} (the initial biomass on “flail harvested fields” (Gill et al., 1996)). This gives $a = 0.00214 \text{ m}^2 \text{ s}^{-1}$ and so $0.00214 \times M^{0.71} / 6050^{0.71}$ (M is body mass in g).

2.4. Depletion

Without grazing, on grassland, sward height decreases during October until February at a constant rate of 0.02 cm d⁻¹ (Bos et al., 2008). Due to grazing, on grassland and wintergreens, sward height further decreases, in case of k species foraging on a parcel according to:

$$(12) \quad \Delta L = \frac{\sum_{i=1}^k N_i I_i}{dA}$$

where N is the number of birds of species i at the parcel and A the area of the parcel (m²). Leaf density d (1298 g m⁻³; (Heuermann, 2007) is used to convert grass and wintergreen biomass intake into length decrement.

On harvest remains, the decrease in resource biomass due to grazing by flocks of k species amounts to:

$$(13) \quad \Delta D = \frac{\sum_{i=1}^k N_i I_i}{A}$$

2.5. Case study

Large numbers of herbivorous migratory waterfowl winter in the Netherlands (Van Eerden et al., 2005). The country has made a commitment laid down in the EU Birds and Habitats Directives to harbour these birds. To solve arising conflicts with agriculture following crop damage inflicted by more than three million wintering birds (van Roomen et al., 2007), national policy changed in 2003. Instead of paying farmers compensation afterwards, areas were designated where farmers were paid beforehand for letting geese and widgeon *Anas penelope* L. forage undisturbed. Outside these so-

called accommodation areas, geese and wigeon could be scared, and under some restrictions be shot (Kwak et al., 2008). The question how much accommodation area should be set aside stirred some debate and estimates ranged from 75,000 (Ebbinghe and van der Gref-van Rossum, 2004) to 150,000 ha (Voslamber et al., 2004). We applied the model to calculate whether the finally proposed 80,000 ha was sufficient for current populations, concentrated at the right locations, and robust in the face of further increases in population size (Nolet et al., 2009). We thus specified distributions of roosting sites and accommodation areas and quantified the resources they contained, and ran the model based on monthly bird census data.

The species involved were: greylag goose *Anser anser* L., white-fronted goose *Anser albifrons* Scopoli, and wigeon *Anas penelope* L., which together cause most damage to agricultural fields and crops, and pink-footed goose *Anser brachyrhynchus* Baillon and barnacle goose *Branta leucopsis* Bechstein that are found in the same areas as the main target species or even occur in mixed flocks (Kwak et al., 2008). According to the observed main food resources of these species in the Netherlands in winter, in the model all geese ate grass and winter cereals (“wintergreens”), with greylag geese also eating harvest remains, whereas wigeon ate only grass (Madsen et al., 1999).

The accommodation areas are a combination of specially designated areas, agricultural fields within Birds Directive sites and grasslands in nature reserves. Vector data (ESRI shape-file format) with the boundaries of the above areas were combined with grid data on land use (LGN5) at a scale of 25 m-squares to arrive at surface areas of four resource types: improved grasslands (109,180 ha), semi-natural grassland (30,651 ha), harvest remains (potatoes and beets, 6104 ha) and wintergreens (cereals, 6187 ha). The total area exceeds the specifically assigned 80,000 ha as it includes also land within Birds Directive sites as well as grasslands in nature reserves. Much of this extra area is

however located far away from roosts, and are therefore not effectively available. Linear elements less than 25 m wide were excluded, as well as contiguous units of <5 ha (Vickery and Gill, 1999).

For grassland, metabolic energy content ($q.e$, where q is the assimilation coefficient and e (J g^{-1}) the energy content of the food) was estimated from the nitrogen concentration (on ash-free dry weight-basis) according to (Prop and Deerenberg, 1991). Field data showed that the digestion of grass does not change in the course of the winter, and that nitrogen content varies per grassland type, but not per region or month (Bos et al., 2008). This gave for improved and semi-natural grassland a metabolic energy content of 7300 and 7200 J g^{-1} , respectively (Bos et al., 2008), both close to the 6700 J g^{-1} of (Prop and Vulink, 1992). The metabolic energy content of the other two food resources was based on literature values: wintergreen $q.e = 0.51 \times 18700 = 9500 \text{ J g}^{-1}$ (Therkildsen and Madsen, 2000; Amano et al., 2004; Hassall and Lane, 2005) and harvest remains $q.e = 0.84 \times 15900 = 13400 \text{ J g}^{-1}$ (Van der Heijden, 1998; Nolet et al., 2002).

As starting value for sward height L we used the height in October, as derived from field measurements (improved grassland 0.094 m; semi-natural grassland 0.066 m; wintergreen 0.06 m) (Bos et al., 2008). Initial biomass of harvest remains was set to 16.4 g m^{-2} (Gill et al., 1996). Note that in the case study, only greylag geese feed on harvest remains.

We took locations of roosting sites for geese from (Koffijberg et al., 1997), classified in size-classes per species as A: 500, B: 2 500, C: 7 500 and D: 20 000 individuals. For wigeon, we used the daytime mid-winter count of January 2006 to determine the locations of wigeon roosting sites, as they rest during the day (data SOVON). The roosting sites were located in the geometric centre of

each main counting area (SOVON and CBS, 2001-2006) with more than 500 wigeons. Roosting site sizes were not classified as for the geese but directly linked to counted numbers.

We obtained the numbers and spatial distribution (per province) of birds from monthly waterfowl censuses. During cold spells the birds move to the south and west, and the coldness of the winter therefore affects the bird distribution. In this paper, we focus on a normal winter, and chose 2005/06 as a representative one (van Roomen et al., 2007). Within each province, geese and wigeon are distributed over the roosting sites in proportion to the roosting population sizes. During the month, distributions stay constant; distribution is updated at the beginning of each month.

Ten primary weather stations in the Netherlands (KNMI) provided daily weather data: mean temperature, mean wind speed at 10 m (20 m in De Bilt), sunshine hours and potential duration of sunshine period (day length). From sunshine data we calculated global radiation using the Ångström formula (Van Keulen and Wolf, 1986). For every km-square in the model, the data of the nearest weather station were used (so, no interpolation was performed).

Because the populations of 4 of the 5 species increased considerably over the last decade, we evaluated a population growth scenario in which for each year after 2005/06 numbers are multiplied by $(1 + \lambda_i)$, where λ_i represents the yearly growth of species i , namely 0.12 for the greylag goose, 0.05 for the white-fronted goose, 0.1 for the pink-footed goose and 0.09 for the barnacle goose (Fig. 4.2 in Van Roomen et al., 2007).

319 2.6. Validation and sensitivity analysis

320 In order to check whether the model produced realistic grazing patterns, we compared model
321 outcomes for the winter 2005/06, a normal winter, with field data collected in 110 km-squares
322 spread over the Netherlands. For 29 of those, from two regions, distance to the roost was available
323 for the field data.

324
325 The observed grazing pressure was calculated from cumulative dropping densities obtained from
326 dropping counts on grassland in 2005-2007 (Bos et al., 2008) and on arable fields in 2006-2008
327 (Visser et al., 2009). In order to express these as bird-days m^{-2} , summed over the winter, dropping
328 densities were divided by the number of droppings per bird per day, based on observed dropping
329 intervals of geese (Ebbinge et al., 1975; Visser et al., 2009) and wigeon (Durant et al., 2006): 135,
330 90 and 85 for geese on grassland, wintergreens and harvest remains, respectively, and 220 for
331 wigeon on grassland. The model gives the total number of goose- and wigeon-days per km-square,
332 summed over the winter. This number was divided by the area of designated grassland or arable
333 field within the km-square to arrive at a grazing pressure in goose- or wigeon-days per square
334 meter.

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336 We also compared the modelled decline in sward height in more than 100 km-squares with the
337 measured sward heights in these squares. Sward height L was measured by throwing a polystyrene
338 disc (24 g, 20 cm diameter) on the vegetation and reading the height from a ruler touching the
339 ground. The average of a minimum of 20 measurements was taken (Bos et al., 2008).

340
341 We investigated the sensitivity of main model results (% deficit) to a limited number of key
342 parameters and assumptions.

Firstly, we tested the effect of a deterministic algorithm for site selection, where the site with best performance is selected (energy balance against minimal costs). We compared the model results under this algorithm with those of a probabilistic approach in which the probability of choosing a site was assumed to scale with its performance defined as $1/DEE$,

$$(14) \quad p_{i,j} = \frac{\frac{1}{DEE_{i,j}}}{\sum_{m,n} \frac{1}{DEE_{m,n}}}.$$

Here $p_{i,j}$ refers to the probability of selecting resource i in cell at location j from the set of available resources m and locations n within the foraging zone around the roost. Results relate to the 2015/16 winter, when considerable depletion is expected.

Secondly, we checked the effect of maximum allowed foraging distance from the roost V_{max} , by varying it over the range 10, 20, 30, 40 and 50 km for geese, and 5, 10, 15, 20 and 25 km for wigeon. This is done for the 2005/06 winter.

Thirdly, we tested the effect of possible overestimation of effectively available resources. One can think of several reasons why not all foraging grounds within accommodation areas can be fully exploited, for instance due to disturbance at the edges or vegetation encroachment in nature reserves. We simulated reduced effective availability by simply decreasing the surface area of resources in all grid cells to 90, 80, 70, 60 or 50% of their original value, again for the 2005/06 winter.

Finally, we modelled a worst-case scenario by taking the 2015/16 winter (after considerable population growth), with probabilistic resource selection, the shortest maximum allowed foraging distance (10 km for geese and 5 km for wigeon), and only 50% effective availability of resources.

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3. Results

White-fronted goose and wigeon are the most numerous species in the Netherlands in winter, also in terms of bird-days on improved grasslands (Fig. 3a). However, due to their larger energy requirement, translated into a larger daily consumption (Fig. 3b), the total consumption of white-fronted geese was calculated to be roughly twice that of wigeon (Fig. 3c). For all species the majority of the consumption is predicted to take place on improved grassland (Fig. 3c).

In the course of the winter, food resources decline as a result of the combined consumption of the species. The model predicts that at the end of the winter (31 March), even in a normal winter like 2005/06, food resources are locally depleted (Fig. 4a).

In a normal winter, shortages are predicted to occur around a few roosts only, mostly situated in the north-west (not shown). With the current numbers, the modelled shortages are small, <1% of the total number of bird-days spent in the Netherlands during the winter (Fig. 5) and mainly occur for greylag goose and wigeon. With increasing numbers, shortages become considerable after 2010 for all species except wigeon (Fig. 5). By 2015/16, the remaining sward length of the main food source shows a decline over a much larger area than 10 years earlier (Fig. 4b).

On grassland, there is agreement between measured and modelled cumulative grazing pressure of geese (all species combined) (Wilcoxon Matched Pairs Test, N = 85, T = 1444, Z = 1.68, P = 0.09) (Fig. 6a). For wigeon, the overall grazing pressure is similar (Wilcoxon Matched Pairs Test, N = 85, T = 1087, Z = 0.91, P = 0.36), although modelled grazing pressure is locally higher than the

measured values (Fig. 6b). In contrast, on arable fields the observed goose grazing pressure seems to show more variation than the modelled one (but small sample size precludes a proper test) (Fig. 6c-d).

Goose grazing pressure decreased curvi-linearly with distance to the roost (Fig. 7a; distance-squared significant in polynomial regression: $t_{26} = -2.32$, $P = 0.028$; $R^2 = 0.42$, $F_{2,26} = 9.33$, $P < 0.001$) ; region not significant in GLM: $F_{1,25} = 0.23$, $P = 0.6$). The model predicts a linear decrease in grazing pressure with distance to the roost (Fig. 7b; $R^2 = 0.50$, $F_{1,27} = 26.5$, $P < 0.0002$; again, region not significant in GLM: $F_{1,26} = 0.15$, $P = 0.7$). However, the distance up to which geese are predicted to forage (8-10 km) is again in agreement with the observations.

Also, the observed decline in sward height in the course of the winter season is well reflected in the model, with observations generally falling within 1 SD of the modelled decline (Fig. 8). In this comparison it should be noted that the initial sward height is calibrated.

In the probabilistic version of the model, differences between runs are negligible (Fig. 9a).

However, compared to the deterministic version, shortages (in winter 2015/16) become higher for greylag, white-fronted and pink-footed goose, and lower for barnacle goose and, especially, widgeon.

When allowing the birds to forage at larger distances from the roost, shortages for greylag goose disappear completely, while they decrease for widgeon (during a normal winter; Fig. 9b). Conversely, decreasing the distance leads to high shortages for all species except pink-footed goose. Highest shortage occurs for widgeon restricted to 5 km.

A reduction of the effective surface of the accommodation areas has a limited effect on the modelled shortages. Only in case of a 50% reduction of the area, shortages of >5% are predicted (during a normal winter; Fig. 9c).

In our so-called worst-case scenario for a normal winter (probabilistic version, with grown population sizes from 2015/16, restricted foraging distances of 10 km for geese and 5 km for wigeon, and 50% effective reduction of available foraging grounds), shortages were considerable: greylag goose 60%, pink-footed goose 36%, white-fronted goose 51%, barnacle goose 60%, and wigeon 26% (SD of the five runs were less than 0.3%, and are not provided).

4. Discussion

4.1. Model behaviour

Model behaviour is to a large extent determined by the assumptions on energy use and acquisition, and in particular by the objectives of the birds. The *minimum rule* we applied differs from earlier objectives used in depletion models, like the *matching rule* or the *maximum rule*. According to the *matching rule*, bird numbers spread over the parcels in proportion to the expected energy gain per parcel. This rule is strictly speaking only optimal for *continuous input* systems (Kacelnik et al., 1992; Milinski, 1994), in which the renewal of food takes place at roughly the same rate as the consumption (Milinski et al., 1995). While being applied to *standing crop* systems, like we are dealing with here, by others (Wilmshurst et al., 1995; Fryxell et al., 2004), we therefore did not use this objective. According to the *maximum rule*, birds should prefer the parcel where they can attain the highest energy gain: they should strive for the greatest difference between energy intake and

energy expenditure (Sutherland and Anderson, 1993). This objective is appropriate in systems where birds try to increase in body weight as fast as possible, as they do during migration (Lindström and Alerstam, 1992). The *maximum rule* will lead to a higher food intake than we modelled here, because the birds aim for maximum net energy intake instead of energy balance. The latter is more likely to be the general pattern during winter, because birds presumably try to avoid to become too heavy as this can have serious costs and risks (Witter and Cuthill, 1993). In reality the birds presumably switch from net energy maximization to energy expenditure minimization in early winter as soon as they have recovered from autumn migration (Nolet et al., 2006), and *vice versa* in late winter in preparation of spring migration (Prop and Deerenberg, 1991; Ebbinge and Spaans, 1995). This latter period is largely kept out of our considerations as we modelled winter until the 31 March. Therefore we believe that the *minimum rule* reflects the behaviour of the wintering birds quite well, and leads to only a slight underestimation of the real energy requirement.

Model behaviour can be understood from Fig. 10, showing for the main resource the range of sward length for which sufficient energy can be acquired to stay in energy balance, depending on distance from the roosting site. Sward length requirements are obtained by numerically solving $MEI(L,V) = DEE(V)$, with L the sward length (m) and V the distance to the roost (m), for birds spending all available time (day length minus flight duration) foraging. The *minimum rule* implies that each species will reduce sward length up to the species-specific minimum value, starting at the nearest locations. With initial sward length set to 0.094 m, the curves indicate that, while for geese grass is energetically available over a large distance, for wigeon shortages may occur at the start of the period because the long swards make the resource's energy yield insufficient. Due to grazing by the other species, sward length decreases, and for wigeon available resources quickly increase through

a process called facilitation. With decreasing sward length, available resources for geese decrease with the declining maximum distance at which the intake balances daily energy demands. However, up to a length of 0.05 m, this decline applies only to distances longer than approximately 30 km, and is therefore largely theoretical. Below 0.05 m, shortages will start to occur, first for greylag, than pinkfoot, white-fronted and barnacle goose and, finally, for wigeon.

The value of V_{max} of 15 km for the wigeon as the smallest considered species (Hedenström, 2008) is in accordance with data from radio-tracked birds (Boudewijn et al., 2009). The maximum foraging distance predicted from energetic requirements (Fig. 10) amounts to approximately 10 km in cold winter nights, which is less than the allowed value (V_{max} of 15 km). The same applies to barnacle goose (26 versus 30 km). For the other goose species, maximum sustainable distance to the roost, as emerging from the model, is much larger than the applied limit of 30 km. Increasing V_{max} for wigeon should have no direct impact on shortages for this species. However, increasing V_{max} simultaneously for all species may have indirect impacts (via lowered competition and/or increased facilitation) as shown in Fig. 9b. From Fig. 10 it follows that lowering V_{max} will severely limit the amount of resources available, and thus result in considerable shortages (Fig. 9b).

Interestingly, the curves of Fig. 10 also explain the difference between the deterministic and probabilistic simulations: in the probabilistic case, choice of foraging location is by definition less optimal, and as a result energy is ‘wasted’, sward length decreases faster, and for the larger birds (greylag, pinkfoot and white-fronted goose) shortages occur earlier and over a longer period. In contrast, for the smaller birds (barnacle goose and especially wigeon), this results in more parcels with short enough swards, and net lower shortages (Fig. 9a). In our model birds compete (Stahl et al., 2006) but can also facilitate each other, for instance when grass grazed down by geese becomes

available for wigeon (Rees, 1990). The smaller species, wigeon and to a lesser extent barnacle goose, have a characteristic decline in intake rate with sward height above a certain optimum (type 4 functional response), causing a preference for short grass (Rijnsdorp, 1986). This is probably the result of a larger selectivity in tall grass. As the grass gets taller, the proportion poorly digestible parts also increases and by increasing selectivity (which costs time), the birds maintain a high digestibility. Another cause for a type 4 functional response can be a decrease in digestibility with sward height (Fryxell et al., 2004; van Langevelde et al., 2008).

Any shortage predicted by the model results from an energy deficiency on the daily budget of the bird involved. However, this does not necessarily translate into starvation or even loss of body weight of the bird. Animals may trade-off energy gain and mortality risk, and have been shown to take higher risks when starving (Brown and Kotler, 2004). Hence, in practice the birds that are confronted with shortages will most likely opt for foraging outside accommodation areas, even if this involves a higher risk of disturbance or shooting.

4.2. Case study

Our model results suggest that currently sufficient land is designated to accommodate wintering geese and wigeon, and that these areas are generally located at proper places. With populations increasing at the current rate, however, considerable shortages are expected in the coming years (Fig. 5). For wigeon, these shortages are relatively small, as no increase in overwintering population of this species is expected and facilitation by geese partly compensates for the increased competition.

The model generally seemed to perform satisfactory, especially for grassland, judging from the agreement between the observed cumulative grazing pressure (on the basis of dropping counts) and the modelled one (on the basis of functional responses), as well as the agreement between measured and modelled within-winter decline in sward height. Because accommodation areas predominantly consist of grassland, this gives confidence that the model is sufficiently accurate to yield useful predictions.

According to the model, wigeons locally concentrate more than observed (Fig. 6b). This may imply that for this species the *minimum rule* forcing the birds to first deplete nearby locations may be too strict. A more plausible explanation is that because wigeon often do not have clear roosts, there is a mismatch between the locations of the assigned roosting sites in the model and the true locations. For arable fields the agreement between observed and modelled grazing pressures was less than for grassland (Fig. 6c and d). This may for one part be caused by the variation in wintergreens on offer, that are being used to varying degree by geese (Visser et al., 2009). For another part, it reflects that we have less knowledge of goose foraging on arable fields than of goose foraging on grassland (Gill et al., 1996; Teunissen, 1996; Therkildsen and Madsen, 2000; Amano et al., 2008).

Our estimates of accommodation capacity may be too optimistic in case we overestimated the effective size of the accommodation areas. A number of factors could lead to an overestimation of the effectively available surface within accommodation areas. Edge and fragmentation effects were partly accounted for by eliminating narrow linear elements and contiguous areas of <5 ha. However, potential disturbance around infrastructure, trees or buildings was not considered, although it is known that goose usage is less near roads (Bos et al., 2008; Jensen et al., 2008) and in the presence of vertical structures (Jensen et al., 2008). The capacity of nature reserves for geese,

and probably also wigeon, has recently declined after encroachment of grassland (Nienhuis, 2005).

For the current numbers, the model outcome proved however to be robust to changes in effective area (Fig. 9c).

We included the most numerous species in the model. However, other wild herbivores occur in the Netherlands in winter, including resident waterfowl species like the mute swan *Cygnus olor* Gmelin, and the exotic Canada goose *Branta canadensis* L. and Egyptian goose *Alopochen aegyptiacus* L.. Many of these species are on the increase, even stronger than the wintering goose species, and their grazing impact may become significant in the near future. Technically, it should be possible to include these species in the model as intake rates of some of these species have been measured (Nolet et al., 2002; Heuermann, 2007), and in any case many of the functional response parameters are allometrically scaled.

Finally, winter weather may change the accommodation capacity, by affecting the birds energetics and distribution, as well as food availability in the case of snow (Nolet et al. 2009). Future climate change may increase the accommodation capacity. Grass growth was not included in the model. Given the predicted climate change, in the future grass growth will presumably stop later in autumn and start earlier in spring (Van der Graaf, 2006). Energy requirements may also be alleviated when winters grow milder. In addition, because geese use temperature-related cues to time their moment of departure (Bauer et al., 2008; Duriez et al., 2009), the birds may react to the change in climate by departing earlier from their wintering grounds. In theory, all these effects should have a considerable positive effect on the capacity of accommodation areas. However, nothing is more difficult to predict than the future, not the least because the birds may change their behaviour as their numbers change. In some cases, for instance, later departures of geese have been noted,

possibly in reaction to increased competition at stopover sites, that they now try to skip by fuelling longer at the wintering grounds (Eichhorn et al., 2009). Because the tool we developed here has a mechanistic basis, we believe it can be applied, albeit with some modifications, to model these new circumstances.

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Table 1. Parameter values of the five species.

	wigeon	barnacle	white-	pink-	greylag
		goose	fronted	footed	goose
			goose	goose	
body mass M (g) ¹	624	1650	2094	2612	3367
<i>grassland and wintergreen</i>					
functional response b_1 (g m ⁻¹)	0.309 ²	0.333 ²	0.246 ³	0.228 ³	0.250 ²
functional response b_2 (g m ⁻¹)	135 ²	76 ²	29 ⁴	21 ⁴	10 ²
functional response c (s m ⁻¹)	3 ⁵	1 ⁵	0.5 ⁶	0.5 ⁶	0 ⁵
minimal cropping time T_{c0} (s)	0.54 ^{2,7,8}	0.48 ^{2,9,10}	0.59 ¹¹	0.59 ¹¹	0.80 ²
maximal chewing rate $R_{\max}$ (g s ⁻¹)	0.011 ²	0.022 ²	0.032 ¹²	0.039 ¹²	0.083 ²
<i>harvest remains</i>					
functional response a (m ² s ⁻¹)					0.00214
basal metabolic rate BMR (J s ⁻¹)	3.16 ¹³	5.18 ¹⁴	6.14 ¹⁵	7.35 ¹⁵	9.02 ¹⁶
span width (m) ¹⁷	0.805	1.385	1.475	1.525	1.635
flight speed v (m s ⁻¹) ¹⁸	17.7	19.0	15.0	18.8	19.2
flight metabolism VMR (J s ⁻¹) ¹⁹	38.2	60.8	76.1	97.7	123.7
max. distance from roost $V_{\max}$ (m)	15 000 ²⁰	30 000	30 000	30 000	30 000

¹ average of adults in winter (Cramp and Simmons, 1977)

² Durant et al., 2003

³ based on allometric relationship: $\log b_1 = -0.332 \log M + 0.493$ ($R^2 = 0.66$, $N = 4$)

⁴ based on allometric relationship: $\log b_2 = -1.49 \log M + 6.40$ ($R^2 = 0.85$, $N = 3$)

⁵ fit on data (Durant et al., 2003)

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- 1 ⁶ interpolation
 - 2
 - 3 ⁷ Jacobsen, 1992
 - 4
 - 5
 - 6 ⁸ Durant and Fritz, 2006
 - 7
 - 8 ⁹ Lang and Black, 2001
 - 9
 - 10 ¹⁰ Van der Graaf et al., 2006
 - 11
 - 12
 - 13 ¹¹ average of other species
 - 14
 - 15 ¹² based on allometric relationship: $\log R_{max} = 0.871 \log M - 4.38$ ($R^2 = 0.84$, $N = 4$)
 - 16
 - 17
 - 18 ¹³ Brunckhorst, 1996
 - 19
 - 20 ¹⁴ Nolet et al., 1992
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 - 23 ¹⁵ based on allometric relationship: $\log BMR = 0.755 \log M - 1.642$ ($R^2 = 0.97$, $N = 9$)
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 - 25 ¹⁶ Bruinzeel et al., 1997
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 - 27
 - 28 ¹⁷ Cramp and Simmons, 1977
 - 29
 - 30 ¹⁸ Clausen et al., 2002
 - 31
 - 32
 - 33 ¹⁹ Norberg, 1996
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 - 35 ²⁰ Boudewijn et al., 2009
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197 **Figure captions**

799 **Fig. 1.** Overview of processes involved in the model.

801 **Fig. 2.** Functional response of five species of herbivorous waterfowl, based on literature data. The
802 intake rate is corrected for alert time. GLG = greylag goose; PFG = pink-footed goose; WFG =
803 white-fronted goose; BAG = barnacle goose; WIG = wigeon.

805 **Fig. 3.** Modelled bird-days, daily consumption per bird and total consumption per species per
806 resource type in a normal winter (2005/06). IG = improved grassland; NG = semi-natural grassland;
807 WG= wintergreen; HR = harvest remains. For species abbreviations see Fig. 2.

809 **Fig. 4.** Modelled remaining sward height in improved grasslands within accommodation areas in
810 the Netherlands with (upper panel) 2005/06 bird numbers, and (lower panel) future bird numbers in
811 2015/16, in a normal winter.

813 **Fig. 5.** Modelled future shortages (% of total bird-days) that cannot be spent inside accommodation
814 areas in the Netherlands for five species (see Fig. 2) increasing at a constant rate. The wigeon
815 overwintering population is kept constant.

817 **Fig. 6.** Comparison of observed and modelled cumulative grazing pressure of geese and wigeon in
818 85 and 24 one-km-squares of grassland and arable fields, respectively. The observed grazing
819 pressure is calculated by dividing the sum of droppings in marked plots by dropping production.

The modelled grazing pressure is the model outcome in bird-days divided by the surface area of grassland or arable field within the one-km-square.

Fig. 7. (a) Observed and (b) modelled relationship between grazing pressure and distance to the roost in 29 one-km-squares. Lines are best-fitting regressions (see text). Upward and downward triangles indicate data from two different regions (not significant in general linear models, see text).

Fig. 8. Comparison of observed (mean) and modelled (mean $\pm$ SD) sward height in improved and semi-natural grasslands in 119 one-km-squares spread over the Netherlands. Data from (Bos et al. 2008).

Fig. 9. (a) Comparison between shortages (% of total bird-days) predicted by deterministic and probabilistic versions of the model, for the 2015/16 (normal) winter (see Fig. 5). The variation between probabilistic runs is very low (SD bars are barely visible). (b) Shortages for the five species for different maximum foraging distances (geese: $V_{max} = 10, 20, 30, 40$ and 50 km; wigeon: $V_{max} = 5, 10, 15, 20$ and 25 km) in a normal winter (2005/06). (c) Modelled shortages of five species (see Fig. 2) in a normal winter (2005/06) as a function of the surface area within accommodation areas that can effectively be used by the geese and wigeon.

Fig. 10. Area between curve and y-axis defines for each species the grass length for which sufficient energy can be acquired, against distance from foraging location to roost. Day and night length set to 10 and 14 hours, respectively. Weather conditions assumed such that actual metabolic rate when foraging $TMR = 2 * FMR$. Other parameters as in Table 1.

Appendix– Calculation of thermoregulation costs

Input variables are the ambient air temperature T_a (°C), windspeed u_{hc} (m s⁻¹) at 10 m height and global radiation R_g (W m⁻²). Output is TMR , the metabolic rate needed to keep a bird body at 40 °C.

$$TMR = H \cdot 4\pi \cdot r^2 \quad (\text{Note: van der Graaf et al. 2001 uses } \pi \cdot r^2)$$

where r (m) is the *radius* of the bird, calculated from body mass M (g) using an empirical relationship (Birkebak 1966 in Van der Graaf et al., 2001):

$$r = \sqrt{((485.6 \times M / 1000 + 592.83) / (4\pi))} / 100$$

and H (W m⁻²) is the *heat flux per surface area*, which in turn is calculated as:

$$H = (\rho \cdot cp) \cdot (T_b - T_{es}) / (r_p + r_e)$$

where

ρ (g m⁻³) is the *density of dry air* as a function of T_a :

$$\rho = 1292 - (5 \cdot T_a) + (0.01567 \cdot T_a^2) \quad (\text{Monteith 1973 in Robinson et al., 1976})$$

cp is *specific heat of air* (1.010 J g⁻¹ °C⁻¹)

T_b is *body temperature* (40 °C)

T_{es} is *standard operative temperature* (°C) (see below)

r_p is *plumage resistance* (867 s m⁻¹) (van der Graaf et al., 2001)

869 r_e (s m⁻¹) is *equivalent outer resistance*:

870
871
$$r_e = (r_r \cdot r_a) / (r_r + r_a) \quad (\text{Robinson et al., 1976})$$

872
873 with:

874 r_r (s m⁻¹) is *radiation resistance*:

875
876
$$r_r = (\rho \cdot cp) / [4 \cdot \varepsilon \cdot \sigma \cdot (T_a + 273)^3]$$

877
878 where

879 ε is *emissivity of the surface* of the bird (0.98) (Cartar et al., 1997)

880 σ is the *Stefan-Boltzmann constant* (5.67 10⁻⁸ W m⁻² °C⁻⁴)

881 r_a (s m⁻¹) is *convection resistance*:

882
883
$$r_a = (r_{fr} \cdot r_{fo}) / (r_{fr} + r_{fo})$$

884
885 with:

886 r_{fr} (s m⁻¹) is *free convection resistance*:

887
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$$r_{fr} = 820 [2 \cdot r / (T_s - T_a)]^{1/4}$$

889
890 and

891 r_{fo} (s m⁻¹) is *forced convection resistance*:

$$r_{fo} = 307 \sqrt{(2 r / u)}$$

where:

u (m s⁻¹) is the wind speed experienced by the bird (see below).

Furthermore:

$$T_{es} = T_b - (1 + 0.26 \cdot \sqrt{u}) \cdot (T_b - T_e) \quad (\text{Bakken, 1990 in Cartar et al., 1997})$$

where:

T_e (°C) is *equivalent temperature*:

$$T_e = T_a + (R_{abs} - R_{emi}) \cdot r_e / (\rho \cdot cp) \quad (\text{Campbell, 1977 in Cartar et al., 1997})$$

in which:

R_{abs} (W) is the *radiation absorbed* by the bird:

$$R_{abs} = \alpha \cdot A_{ratio} \cdot R_g + \epsilon_s \cdot \sigma \cdot (T_a + 273)^4 \quad (\text{Campbell, 1977 in Cartar et al., 1997})$$

where:

α is *absorbtivity to radiation* (0.75) (Calder & King 1974 in (Robinson et al., 1976))

A_{ratio} is *relative surface receiving direct radiation* (0.29) (Cartar et al., 1997)

ϵ_s is *emissivity of the surroundings* (0.94) (Cartar et al., 1997)

R_{emi} (W) is the *radiation emitted* by the bird:

$$R_{emi} = \varepsilon \cdot \sigma \cdot (T_s + 273)^4 \quad (\text{Campbell, 1977; note: Cartar et al., 1997 give } T_b)$$

918

919 The wind speed u (m s^{-1}) at the bird level is:

920

$$u = u^* / k_v \cdot [\ln ((h_b + z_m - pd_0 \cdot h_v) / z_m)] \quad (\text{Campbell, 1977 in Cartar et al., 1997})$$

922 where:

923 u^* (m s^{-1}) is *friction velocity*:

924

$$u^* = u_{hc} \cdot k_v / [\ln ((h_c + z_m - pd_0 \cdot h_v) / z_m)] \quad (\text{Campbell, 1977 in Cartar et al., 1997})$$

926 with:

927 u_{hc} is the wind speed measured at height h_c ($h_c = 10$ m)

928 k_v is the *Von Karman proportionality constant* (0.41) (note that k_v cancels out in u^* equation)

929 z_m is *roughness length* (0.01 m) (Wieringa, 1993 in Van der Graaf et al., 2001)

930 pd_0 is *relative displacement height* (0.78 of h_v) (Shuttleworth, 1989 in Van der Graaf et al., 2001)

931 h_v (m) is *vegetation height* (0.05 m)

932 h_b (m) is *height of the bird's centre of gravity above the ground*, derived from r (bird radius): $h_b =$

933 $1.5 \times r$

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Figure

Fig. 1.

Fig. 2.

Fig. 3.

Cultuurgras, lengte (m)

Cultuurgras, lengte (m)

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.