

Discriminating between possible foraging decisions using pattern-oriented modelling: The case of pink-footed geese in Mid-Norway during their spring migration



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ABSTRACT

Foraging decisions and their energetic consequences are critical to capital Arctic-breeders migrating in steps, because there is only a narrow time window with optimal foraging conditions at each step. Optimal foraging theory predicts that such animals should spend more time in patches that enable them to maximise the net rate of energy and nutrient gain. The type of search strategy employed by animals is, however, expected to depend on the amount of information that is involved in the search process. In highly dynamic landscapes, animals are unlikely to have complete knowledge about the distribution of the resources, which makes them unable to forage on the patches that enable them to maximise their net energy intake. Random search may, however, be a good strategy in landscapes where patches with profitable resources are abundant. We present simulation experiments using an individual-based model (IBM) to test which foraging decision rule (FDR) best reproduces the population patterns observed in pink-footed geese during spring staging in an agricultural landscape in Mid-Norway. Our results suggested that while geese employed a random search strategy, they were also able to individually learn where the most profitable patches were located and return to the patches that resulted in highest energy intake. Such asocial learning is rarely reported for flock animals. The modelled geese did not benefit from group foraging, which contradicts the results reported by most studies on flocking birds. Geese also did not possess complete knowledge about the profitability of the available habitat. Most likely, there is no one single optimal foraging strategy for capital breeders but such strategy is site and species-specific. We discussed the potential use of the model as a valuable tool for making future risk assessments of human disturbance and changes in agricultural practices.

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1. Introduction

The movement strategy that animals use while foraging on spatially dispersed resources is crucial to their success in exploiting them (Viswanathan et al., 1999; Bartumeus et al., 2005; Giuggioli and Bartumeus, 2010). Foraging decisions and their energetic consequences are particularly important to capital Arctic-breeders migrating in steps, as they only have a narrow time window with optimal foraging conditions at each step. Hence, the spring migration is regarded as an energetic bottleneck in the annual cycle of capital breeders (Ankney and MacInnes, 1978; Alerstam and

Lindström, 1990; Ebbinge and Spaans, 1995; Prop and Black, 1998; Drent et al., 2003) that have to garner body stores in order to start breeding soon after arrival on the breeding grounds. Optimal foraging theory predicts that such animals should spend more time in patches that enable them to maximise the net rate of energy and nutrient gain (Killen et al., 2007; Hedenström, 2008; Bartumeus and Catalan, 2009; Stephens et al., 2014). In heterogeneous, dynamic landscapes where the availability and quality of food resources vary both spatially and temporally, foraging at the most profitable patches requires that the animals have a complete knowledge about the environment, which is rarely the case and it has been widely suggested that foraging animals possess incomplete rather than complete knowledge about their landscapes (Bernstein et al., 1988; Pettifor et al., 2000; Koops and Abrahams, 2003; Amato et al., 2006a; Nolet et al., 2006; Bartumeus and Catalan, 2009; Matsumura et al., 2010; Kułakowska et al., 2014). The type of search strategy

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employed by animals therefore strongly depends on the amount of information that is available in the search process. Random searching is a profitable strategy when information is lacking, confusing or difficult to gather (Bernstein et al., 1988; Bartumeus and Catalan, 2009). Animals can also learn where the profitable patches are located and return to the same area or the vicinity of that area for consecutive foraging bouts (Charnov, 1976; Amano et al., 2006b). Migrants can acquire information about resource availability, distribution and predation/disturbance risk directly through their own experience (asocial learning) or indirectly by observing or exchanging information with other conspecifics (social learning), which may be of particular importance for animals migrating in flocks. Social learning may provide a shortcut to information acquisition and at the same time allows individuals to avoid time consuming and risky exploratory behaviour. However, social information is potentially less reliable, especially when resources are very dynamic and/or patchy (Németh and Moore, 2014), than information gathered personally (asocial learning), largely due to its second-hand nature (Németh and Moore, 2007), but it may be favoured if obtaining information individually is costly or if migrants are time-restricted and opt for fast fuelling rate. Group foraging, a key element of social learning, has been demonstrated as an important factor in foraging decision making of various species (Amano et al., 2006a; Kułakowska et al., 2014), however, little is known about the role of asocial learning, especially for species frequently observed in flocks.

Besides the nutritional and energetic content of the available food resources, animals searching for optimal foraging sites need to consider other factors such as the costs related to searching and movement, predation or disturbance risk, and inter- and intraspecific competition because these aspects may significantly reduce their intake rate (Lindström, 1990; Moore and Yong, 1991; Ydenberg et al., 2002; Olsson et al., 2008; Wood et al., 2013). Disturbance, which can also be regarded as predation risk (Beale and Monaghan, 2004; Tombre et al., 2005; Klaassen et al., 2006), might be an important factor influencing foraging behaviour of animals that forage in agricultural landscapes, as they are likely to be frequently exposed to human activities and/or their presence may conflict with agricultural interests. Disturbance can cause both an increase in energy expenditure by forcing animals to frequently move away from the source of disturbance, and a decrease in energy intake by preventing them from foraging in the disturbed area (Madsen, 1994; Klaassen et al., 2006; Stillman et al., 2015). It can be argued that due to large number of factors influencing foraging behaviour of animals, a wide variety of strategies may be optimal and such strategies are, most likely, environment- and species-specific (Turner et al., 1993; Gross et al., 1995).

Understanding the relationship between processes, adaptive traits of individuals and patterns, so called bottom-up approach, is fundamental to our understanding of the behaviour and ecology of a species. Bottom-up simulations, as opposed to top-down approaches, allow the processes and mechanism behind the observed patterns to be revealed. Individual-based ecology provides a conceptual framework where populations and ecosystems are viewed as complex systems with properties that emerge from the traits and interactions of their lower-level, individual components. Modelling often allows for revealing patterns which are difficult to directly observe in nature, like learning processes of animals. Several studies attempted to uncover the role of different factors affecting the distribution and foraging decisions of animals through an individual-based modelling approach (Amano et al., 2006a; Wood et al., 2013; Kułakowska et al., 2014; Nabe-Nielsen et al., 2014). For example, models by Amano et al. (2006a) and Kułakowska et al. (2014) revealed the importance of group foraging in decision making of birds.

We present simulation experiments using individual based models (IBMs) to test the potential decision making rules and the mode of acquiring information in Svalbard-breeding pink-footed geese during their spring migration in a key stopover site in Mid-Norway, where the availability of different food resources is very dynamic (Chudzińska et al., 2015) and geese are under pressure to store energy and continue migration towards the breeding area. Hence, the setting offers an interesting possibility to test optimal foraging hypotheses and trade-offs including foraging on different habitat types according to their availability (random search), maximising energy intake by foraging on highly energetic habitat patches, which requires from birds complete knowledge about the environment, and choosing foraging patches based on asocial and/or social learning. We also investigate how disturbance, intraspecific competition and physiological constraints influence foraging behaviour, energetics and spatiotemporal distribution of geese. To do so, we model five different foraging decision rules (FDR): (1) random selection of fields, where animals do not gain experience, (2) completely informed geese, (3) non-omniscient foragers that gain familiarity of the environment through experience, (4) non-omniscient socially learning foragers and (5) non-omniscient but learning, both socially and through experience. In each foraging decision rule geese are exposed to various disturbance levels corresponding to those found in nature. They compete with each other for resources, and their foraging is constrained by physiological aspects. The five FDRs are defined in search of a single optimal foraging decision rule, which is the best practice according to the specific environment in Mid-Norway and energy requirements of the geese. Following a pattern-oriented modelling (POM) strategy (Grimm et al., 2005; Railsback and Grimm, 2012), we test the capacity of the five aforementioned alternative foraging decision rules to reproduce five population level patterns observed in nature. In POM, patterns observed in real systems at different hierarchical levels and scales are used to optimise model complexity, reduce uncertainty and test and contrast theories (Grimm et al., 2005). The contrasted patterns include changes in daily net energy intake within the stopover season, how much of the potential time available for foraging geese spend resting, phenology of geese, spatiotemporal changes in goose distribution and number of geese observed at roost sites during their stay in Mid-Norway. The observed patterns are based on long-term studies and detailed satellite tracking of pink-footed geese in Mid-Norway.

2. Materials and methods

2.1. Study population and site

The Svalbard-breeding population of pink-footed geese overwinters in Belgium, The Netherlands and Denmark. During their migration to the breeding grounds the geese stop in Trøndelag in Mid-Norway, and Vesterålen in North-Norway (Madsen et al., 1999; Fig. 1). The geese start arriving in Mid-Norway in early April, and numbers peak during late April–early May (Madsen et al., 1999). Individual geese stay in Mid-Norway for an average of 20 days before migrating further north (Bauer et al., 2008).

The study site in Mid-Norway is semi-mountainous and characterised by a patchwork of agricultural fields and forests. The area is rich with lakes and coastal areas, both of which serve as roost sites for the geese (Fig. 1). Based on data from satellite tagged pink-footed geese at the study site and long-term observation of this species in Mid-Norway, pink-footed geese are mainly observed foraging within 5 km from the roost sites, and 93% of all agricultural fields within the study site is located within 5 km from a roost site (Jensen et al., 2008; Chudzinska, unpubl. manuscript). We therefore chose 5 km as the maximum search radius of the modelled

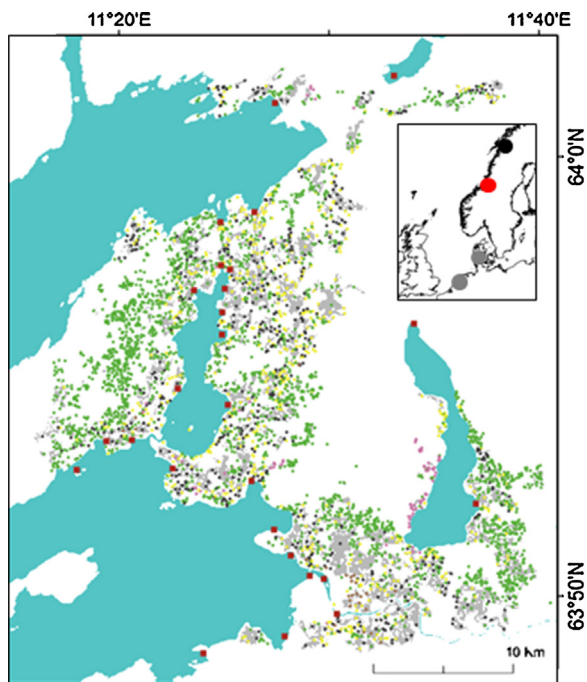


Fig. 1. The initial model landscape of the Mid-Norway stopover site with different habitat types represented by dots (grass—green, stubble—yellow, ploughed—black, potato—brown and others—pink). Roost sites are represented by red squares, water by blue and the actual shape of the agricultural fields are shown in grey in the background. The map in the top right corner shows spring migration flyway of pink-footed geese: wintering areas in the Netherlands/Belgium and Denmark (grey dots), study site (red dot) and the final stopover site in North-Norway (black dot). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

geese. Geese are rarely seen resting on the fields and therefore the above-mentioned roosting sites constitute their main resting places (Madsen et al., 1997). Roost sites are also the main source of drinking water. The number of geese at each roost site and the positions of these sites are monitored in Mid-Norway every year by trained observers. The day length increases by 4 h over the stopover season, and because the geese feed exclusively during daytime hours (Madsen et al., 1997), the time available for foraging increases accordingly. There are four main foraging habitats available to geese: grass, barley stubble from the preceding autumn, newly sown/germinating barley grains and ploughed barley stubble, but geese also occasionally forage on waste potato fields. These habitats are henceforth referred to as grass, stubble, grain, ploughed and potato. Time-activity budgets for pink-footed geese in Mid-Norway conducted by the authors revealed that ploughed fields are mainly used as resting sites. Grass is widely available during the entire stopover season and it starts growing at the end of April (Bjerke et al., 2014). Stubble fields are gradually ploughed and subsequently sown with barley, which starts germinating towards the end of the stopover season (Madsen et al., 1997). To study changes in behaviour and energetics of geese over the stopover season, we divided it into four periods, which roughly corresponded to habitat changes due to agricultural practices. Period 1 was from 6th–25th April, period 2: 26th April–3rd May, period 3: 4th–11th May and period 4: 12th–19th May. The position, size and habitat type of each field was derived from regular habitat mapping conducted during fieldwork in 2013 (Chudzińska et al., 2015).

The foraging behaviour of herbivores like pink-footed geese is influenced by their digestive constraints (Demment and Van Soest, 1985; Kvist and Lindström, 2000). Geese therefore feed as long as it takes them to fill their guts (time of the first passage), and stop feeding until the food in the gut is processed (retention time) (Bednekoff

and Houston, 1994). Time of the first passage has been estimated to be between one and four hours for geese feeding on graminoids (Dorozunskia, 1963; Marriot, 1970; Burton et al., 1979). For geese, the mean retention time is 2–3 h for grass (Burton et al., 1979) and probably less than 2–3 h for grain, which is digested faster than grass due to its lower cellulose content (Demment and Van Soest, 1985). Geese at the study area prefer to rest and digest food on roost sites rather than staying on fields, probably to avoid disturbances (Chudzińska, unpubl. manuscript).

Pink-footed geese at the study site are exposed to various disturbing events (intentional scaring, passing cars, dogs etc.). Studies conducted at the study site (Jensen et al., 2008; Chudzińska et al., 2013) and in Denmark (Madsen, 1985a), showed that geese tend to forage at places further away from roads and thus on larger fields (generally $>0.06 \text{ km}^2$). Geese flee as a reaction to a disturbance at an average distance of 120 m and after being disturbed, geese are likely to fly directly to a roost site if such a roost site is within a short distance (Madsen, 1985a).

Flock sizes of 10–20 individuals were most common during a survey conducted in 2012 (Chudzińska, unpubl. manuscript). Each modelled goose represents therefore 20 individual geese.

2.2. Model description

We developed a spatially explicit individual-based model (IBM) that tracks the hour-to-hour spatiotemporal distribution of geese and the dynamics of energy stores of each individual throughout the stopover season, until the animals leave the study site. The model description follows the updated ODD (Overview, Design concepts, Details) protocol suggested by Grimm et al. (2006, 2010). The model was programmed in NetLogo 5.0.4 (Wilensky, 1999).

2.2.1. Purpose

The purpose of the model is to investigate how pink-footed geese decide which fields to forage in during spring migration. It explicitly incorporates memory, disturbance, physiological constraints, energetics and intraspecific competition and produces a range of emergent patterns that depend on the choice of foraging decision rule (FDR).

2.2.2. Entities, state variables and scales

2.2.2.1. Entities and state variables. The IBM includes three kinds of agents: geese, roosts and fields.

Goose agents are characterised by their location, energetics (kJ h^{-1}) (amount of metabolised energy intake, energy expenditure and net energy intake rate), and time of the first passage time (h) (cumulative time spent feeding during a particular day until returning to a roost site). Each goose agent represents 20 individual geese (each referred to as a super goose from now on) (Scheffer et al., 1995).

Roosts (resting places located on water) are represented as immobile agents characterised only by their location. The model includes all 26 roost sites in the study area (Fig. 1).

Fields: The model world includes all agricultural fields within 5 km from the roost sites, which is the area where most geese forage (Jensen et al., 2008; see also Section 2.1 for details). The fields are represented by immobile agents with positions corresponding to the centres of the agricultural fields in the study area [field centres obtained using Arc GIS (ESRI, 2010)]. They are characterised by their location, size (m^2), habitat type (a field can be one of five habitat types: grass, stubble, grain, ploughed or potato) (Fig. 1) and biomass (g per field). The relative proportion of the habitat types changes at the beginning of each of the four periods (see Section 2.1; Table 1).

2.2.2.2. Scales. Simulations are based on a $28.5 \times 33.8 \text{ km}^2$ landscape covering an area between Steinkjer, Verdal and Inderøy

Table 1
Values of input parameters used in the analysis of foraging behaviour of pink-footed geese spring staging in Mid-Norway. The detailed description of the sub-models (marked with bold font) is given in Appendix A. Values are shown as mean \pm SD where applicable.

Description	Unit	Value	References
Initialisation			
Initial grain density (D)	g m^{-2}	22 ± 22 (stubble); 17 (grain)	Baveco (unpubl. manuscript) and Jensen et al. (2012)
Initial compressed sward length	m	0.03 (at the start of the model), 0.01 (for the newly sown grass)	Baveco (unpubl. manuscript) and Bjerke et al. (2014)
Initial compressed sward length of newly sown grass fields	m	0.01	
Large/small fields threshold	km^2	0.06	Chudzińska et al. (2014) and Madsen (1985)
Initial body stores	kJ	22048 ± 3107 (equivalent to $\text{API} = 2 \pm 0.5$)	Drent et al. (2003) and Madsen et al. (1997)
Number of grass patches		2455 (period 1); 2389 (period 2); 2334 (period 3); 2274 (period 4)	Chudzinska (unpubl. manuscript)
Number of grain patches		0 (period 1); 153 (period 2); 773 (period 3); 1269 (period 4)	Chudzinska (unpubl. manuscript)
Number of stubble patches		578 (period 1); 272 (period 2); 76 (period 3); 20 (period 4)	Chudzinska (unpubl. manuscript)
Number of ploughed patches		554 (period 1); 842 (period 2); 491 (period 3); 116 (period 4)	Chudzinska (unpubl. manuscript)
Number of potato patches		27 (period 1); 20 (period 2); 5 (period 3); 1 (period 4)	Chudzinska (unpubl. manuscript)
Number of other patches		86 (period 1); 24 (periods 2); 21 (period 3); 20 (period 4)	Chudzinska (unpubl. manuscript)
Grass growth			
Grass growth	cm day^{-1}	0.038 (period 1); 0.126 (period 2); 0.279 (period 3); 0.459 (period 4)	Bjerke et al. (2014)
Intake rate and updating energetics			
Time of the first passage	h	3	Parameterised
Energy expenditure (EE)	kJ h^{-1}	54.28 (roost sites and fields); 416.35 (flying)	Chudzińska (unpubl. manuscript) and Butler and Bishop (1999)
Average flight speed	km h^{-1}	50	Fox et al. (2003) and Green et al. (2002)
Proportion of time step spent on feeding (mean \pm SD) (t_f)		0 (roost sites and ploughed); 0.66 ± 0.12 (grass, stubble, potato); 0.78 ± 0.08 (grain)	Chudzińska et al. (2013)
Gross energy content of food (GF)	kJ g^{-1}	16.18 (grass); 14.55 (grain); 17.24 (stubble)	Chudzińska (unpubl. manuscript)
Gross energy content of droppings (GD)	kJ g^{-1}	12.82 (grass); 11.47 (grain); 13.97 (stubble)	Chudzińska (unpubl. manuscript)
Dropping production rate (DR)	h	9.8 (grass); 4.5 (grain); 5.6 (stubble)	Chudzińska (unpubl. manuscript)
Metabolised energy intake on potato fields	kJ h^{-1}	879.5	Baveco (unpubl. manuscript)
Regression coefficient 1 (b_1)		0.28	Baveco (unpubl. manuscript)
Regression coefficient 2 (b_2)		9.6	Baveco (unpubl. manuscript)
Regression coefficient 3 (b_3)		2.8	Baveco (unpubl. manuscript)
Cropping time (t_c)	H	1512	Baveco (unpubl. manuscript)
Maximum rate of chewing (R_{\max})	g h^{-1}	30.6	Baveco (unpubl. manuscript)
Attack rate (a)	$\text{m}^2 \text{h}^{-1}$	11.7 (stubble); 5.87 (grain);	Baveco (unpubl. manuscript)
Handling time (H)	h g^{-1}	0.022 (stubble); 0.050 (grain)	Baveco (unpubl. manuscript)
Leaving a field			
Small radius	km	1	Amano et al. (2006a,b)
Memory factor (α)		0.07	Parameterised
Probability of disturbance	%	0 (nights and day roost sites); 30 (on fields $\leq 0.06 \text{ km}^2$); 20 (on fields $> 0.06 \text{ km}^2$)	Chudzińska (unpubl. manuscript)
Roost-disturbance radius	km	1	Parameterised
Leaving the model			
Starvation energy stores threshold	kJ	9620 (equivalent to a goose with $\text{API} = 0$)	Madsen and Klaassen (2006)
Moving north energy stores threshold	kJ	45036 ± 2128 (equivalent to $\text{API} = 4.25 \pm 0.25$ and accounted for efficiency for utilisation metabolisable energy intake (0.8))	Drent et al. (2003), Duriez et al. (2009) and Lopez and Leeson (2008)

municipalities in the County of Nord-Trøndelag in Mid-Norway. The model's spatial extent is 571×675 grid cells, each covering $0.05 \times 0.05 \text{ km}^2$ (Fig. 1). The model runs in 1-h time steps from mid-night 6th April 2012, when the first geese arrive, and ends 20th of May, or when all geese have migrated north or starved to death.

2.2.3. Process overview and scheduling

Before the simulation starts, a foraging decision rule (FDR) is selected. At each midnight of each simulation day between the first

(6th April) and middle (30th April) days of the simulated stopover season, new geese arrive at a random roost site in the study area. Since pink-footed geese only forage during daytime (Madsen et al., 1997), modelled geese leave roost sites in the morning after civil twilight, which is considered as the beginning of each day. They forage in the fields during daytime and come back to roost sites at sunset. Depending on the FDR, geese follow different procedures that define which fields to forage on and which roost site to return to either after sunset or for a rest during daytime. Geese do not

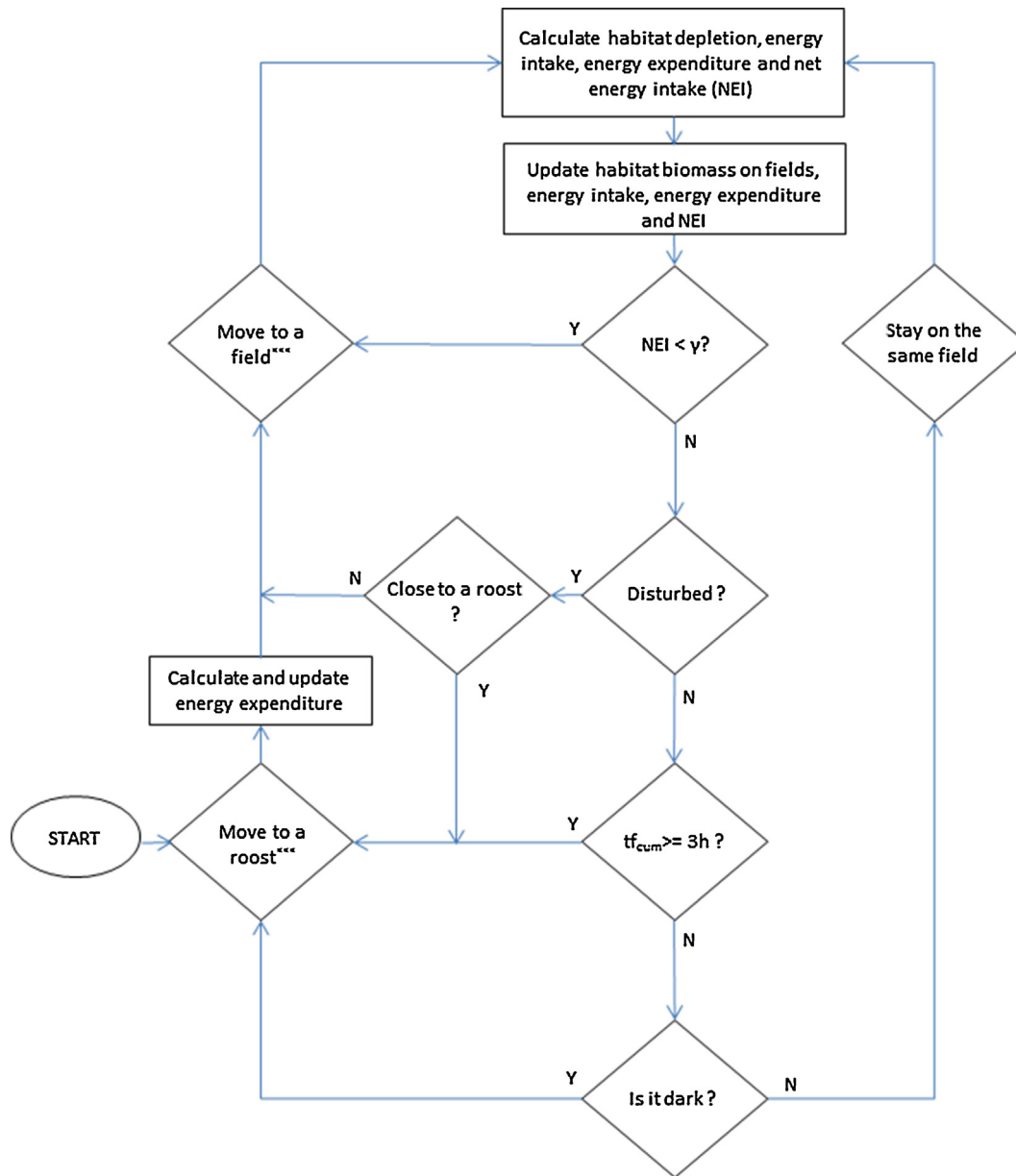


Fig. 2. Flow diagram describing the general daily foraging decision of pink-footed geese under all foraging decision rules. Diamond-shaped symbols indicate decisions made by geese and rectangles indicate calculations. γ is the expected gain rate and tf_{cum} cumulative time spent feeding from leaving a night roost to a current time step. *** a goose's decision which roost or field to move to is the foraging decision rule-specific.

move between fields within a time step. Each time step the below actions happen in sequence. Each super goose goes through all the actions and afterwards next goose proceeds. The order of the geese is randomised at every time step. The graphical description of the model flow is shown in Fig. 2.

2.2.3.1. Update field types and energy content. At the time step when a new period begins (see Section 2.1) habitat type on each field is updated to mimic habitat change due to agricultural practices observed in nature. The biomass of new fields is calculated based on field size and habitat type.

2.2.3.2. Goose arrival. On each modelled day, an empirically derived number of super geese arrive to the model until 30th of April.

2.2.3.3. Grass growth. Grass fields increase their forage biomass.

2.2.3.4. Intake rate and habitat depletion. If on a field, the super goose forages and depletes the habitat proportionally. The intake rate is habitat specific.

2.2.3.5. Updating energetics. Each super goose spends energy proportionally to the distance it had to fly from the previous field/roost visited and to the time spent on the current field or roost. It gains energy proportionally to the amount of food consumed on the current field. This amount is dependent on the time goose spends feeding and being vigilant, and to the number of other super geese present on a given field at the same time. These factors aim at representing general intraspecific competition and density-dependant processes (see Appendix A for more details).

2.2.3.6. Leaving a field. Each super goose decides whether to stay or leave a given field if one or more of the four field leaving rules are met (see section *Leaving a field* in Appendix A): (1) it abandons a field if the current gain rate falls below the expected gain rate based on its previous experience, (2) it has been foraging continuously for a time necessary to fill its gut (time of the first passage) and therefore need to take a digestive break, (3) it is disturbed or (4) it is sunset and the super goose returns to a roost site.

2.2.3.7. Leaving the model. If a super goose obtains an energy level that is sufficient to migrate north, it leaves the model. It also leaves the model if it cannot obtain energy stores above a starvation threshold (it dies).

2.2.4. Design concepts

2.2.4.1. Basic principles. This model builds on the assumption that geese optimise their foraging behaviour to prepare for further migration and breeding. They do this by intensive foraging on high quality food, reduction in energy expenditure and avoidance of perceived predation risk. The model therefore poses a classical optimal foraging problem: how should an individual decide where to forage to maximise its fitness? We provide insight into this problem by contrasting five alternative theories for this decision based on how well they reproduce the observed pattern.

2.2.4.2. Emergence. The net energy intake of geese emerges from a balance between metabolisable energy intake obtained by foraging on different fields and energy expended during flying between fields/roost sites, activity while in the field, as well as energy used to maintain basic body functions. The amount of time geese spend on roost sites during daytime emerges from their need to digest after having foraged and from their response to disturbances. The amount of time geese need to digest is proportional to the amount of time they spend feeding on fields. The spatial distribution of birds emerges from their tendency to move to different fields at different distances from the roost sites and from the field they originate from, from the spatial distribution of the fields, and from resource depletion. The number of geese at the study site emerges from a balance between new geese arriving to the model and geese leaving the model by either migrating north or starving to death. Geese choose a roosting site for a rest according to different rules specified for each FDR. These choices determine how many geese rest at each roosting site.

2.2.4.3. Adaptation. Geese's habitat selection behaviour (i.e., the decision of which field to occupy every time step to forage on) is the only modelled adaptive trait.

2.2.4.4. Objectives. While animals attempt to optimise their foraging behaviour differently for each foraging decision rule, the overall objective of the geese is to optimise their foraging behaviour to obtain enough energy stores to migrate farther north and to breed. For all FDRs predation/disturbance risk is an important factor perceived by birds: geese choose disturbance-free roost sites as their primary resting places.

2.2.4.5. Learning. In FDRs 3 and 5 geese learn where the most profitable fields are located.

2.2.4.6. Prediction. When geese arrive to the model, they are assumed to already have some knowledge about the profitability of different habitat types and to be able to predict the expected gain rate on their first choice of foraging patch (see Section 2.2.7).

2.2.4.7. Sensing. In all FDRs geese are able to sense the habitat quality of fields within 5 km radius. In FDR 2-max energy geese are able to sense where the most profitable fields are located. In FDRs 2–5 geese are able to sense the distance between their current location and the closest roost site. In FDRs 4 and 5, geese are able to sense which fields within a certain radius are already occupied by other individuals.

2.2.4.8. Interaction. The modelled birds interact indirectly via their competition for food. In FDRs 4 and 5 geese forage in places where other geese are already present.

2.2.4.9. Stochasticity. The initial amount of grain varies stochastically between stubble fields. When geese arrive to the model, they distribute themselves randomly among roost sites and they have their initial energy stores and the amount of energy necessary to leave the model assigned within the ranges given in Table 1. During each run, the values of the following parameters are set randomly: the next field or roost (in FDRs 1, and 3–5), proportion of time spent feeding and being vigilant on each field, number of time steps geese stay on a roost site when following field leaving rules 2 and 3 (see section *Leaving a field* in Appendix A), probability of a super goose being disturbed from a field.

2.2.4.10. Observation. The number of animals, their net energy intake, and total time spent on roost sites during daytime are recorded at the end of each day. The distance of geese to the closest roost site (if geese are on a field) is recorded at each step. The number of geese occupying each roost site is recorded at each time step.

2.2.5. Input data

Two input data files from external sources are used in the model: number of new super geese arriving to the model and distribution of habitat types within the modelled area. The number of arriving geese was assessed based on counts of geese on the roost sites in the years 2005–2012 and new geese arrive to the model as described in Section 2.2.3 and Appendix A. New habitat map is loaded to the model at the beginning of each period as described in Section 2.2.3 and Appendix A. The position, size and habitat type of each field was derived from regular habitat mapping conducted during fieldwork in 2013 (Chudzińska et al., 2015) (Appendix A).

2.2.6. Sub-models

A description of the sub-models corresponding to the processes listed in Section 2.2.3 presented in Appendix A.

2.2.7. Initialisation

The model is initialised by loading a habitat distribution map in the beginning of period 1 and by assigning habitat biomass, grass length or grain density to each field agent (Table 1). As observed in the field, initial grass length and initial grain density on new sown fields do not vary between the fields whereas there is a large variation in grain density on stubble fields. The initial number of birds is set to 7040 geese (352 super geese) that are randomly distributed among roost sites. This is an average number of geese observed at 6th of April based on counts of geese on the roost sites in the years 2005–2012 (Appendix A). Each super goose has a realistic initial energetic value randomly assigned within a range specified in Table 1.

We assume that geese arriving to Mid-Norway have some knowledge about profitability of available habitat types based on experience from the previous years and previous stopover sites (e.g. Madsen, 2001; Kanarek et al., 2008). We therefore

calculate the initial, expected gain rate (see section *Leaving a field* in Appendix A), when geese arrive to the model as follows:

$$\gamma_{in} = ME_{in} - EE \quad (1)$$

Here the initial metabolised energy intake rate (ME_{in}) was calculated as in Eq. (A4) (Appendix A) and energy expenditure (EE) was calculated as the average energy expenditure for all fields (Table 1). The intake rate used to estimate ME_{in} was calculated as an average intake from all fields within a 5-km radius from the roost site that the super goose arrived to for FDRs 1 and 3–5. Since in FDR 2 geese are expected to have a complete knowledge about profitability of each habitat type, only fields where the habitat-specific intake rate was >0 were used to calculate ME_{in} . The intake rate from ploughed fields was therefore excluded from the calculation of the average intake from all fields within 5 km.

2.3. Real world patterns compared to emergent properties of the model

To evaluate which foraging decision rules best characterise the foraging behaviour of pink-footed geese we analysed whether each rule caused the model to reproduce a range of patterns observed in the field in 2005–2007 and 2011–2013. We list the patterns in the order of decreasing importance:

- (1) The average daily net energy intake (daily metabolisable energy intake—daily energy expenditure) of pink-footed geese was $1706 \pm 351 \text{ kJ day}^{-1}$ (mean \pm SD) and this value did not differ between periods (Chudzińska, unpubl. manuscript).
- (2) Geese spent approximately 40% of their time available for foraging (i.e., the daytime hours) on roost sites during the first half of the stopover season and around 25% of daytime in the second half (Chudzińska, unpubl. manuscript).
- (3) The spatial distribution of geese fluctuated diurnally and between periods in response to changes in goose densities at these two time scales. In periods 1 and 4, when the number of geese at the stopover site was lowest, the diurnal distribution of geese did not depend on distance from nearest roost site; geese were observed at the same distance from the roost sites throughout the day. During periods 2 and 3, when densities of geese at the stopover site was highest, the probability of using areas further away from roost sites declined in the morning but increased in the evening. In the mornings, when all geese left the roost sites to forage they had a higher relative probability of staying close to the roost. At middays, when densities on fields were lowest because most geese were roosting, geese used habitat independently of the distance to the nearest roost site. In the evenings, when densities increased again, geese selected areas further away from the roosts (Chudzińska et al., 2015).
- (4) Geese departure from Mid-Norway based on weekly counts in years 2005–2007. The number of geese peaked at the end of April and all geese left by 20th May (Baveco, unpubl. manuscript).
- (5) Maximum number of geese observed at each roost site based on counts conducted between 15th April and 8th May 2013 (Baveco, unpubl. manuscript).

2.4. Geese foraging decisions

We test the model's ability to reproduce the observed patterns (Section 2.3) using five alternative foraging decision rules (FDRs) that differ in complexity. In each FDR, each super goose forages on the fields between sunrise and sunset, but which field it chooses to forage on differs between FDRs. For each FDR, each super goose stays on a field until conditions of one of the four field leaving rules

are met (see Section 2.2.3 and Appendix A), and then moves to the next field or a roost site. The factors that force birds to leave a field and define four leaving rules such as gain rate, physiological constraints, disturbance and darkness do not differ between FDRs. Geese search for their foraging fields within a relatively large area in the morning (5 km as shown by Jensen et al. (2008); termed 'large displacement radius'); however, once they get familiar with their foraging area, they restrict their search to a smaller radius of 1 km (termed 'small displacement radius') (Turner et al., 1993; Gross et al., 1995; Amano et al., 2006a).

2.4.1. Foraging decision rule 1: Random (hereafter, FDR 1-random)

This foraging decision rule was developed following a random search approach as described by Bartumeus and Catalan (2009). In this model, individuals are assumed to have no prior information of the profitability of available fields except at the time when they arrive to Mid-Norway, when they have a certain expected gain rate, presumably based on their experience from previous year (see Section 2.2.7). Each field within a certain radius is equally likely to be chosen by a super goose irrespective of whether it has been visited before and regardless of the biomass of this field. Each super goose leaves the roost after civil twilight and moves to a random field within 5 km from this roost. It forages on this field until leaving according to field leaving rules 1–4 (see section *Leaving a field* in Appendix A, Table 2).

2.4.2. Foraging decision rule 2: Maximising nutrient intake—Omniscient birds (hereafter, FDR 2-max energy)

This foraging decision rule was developed following a rate-maximising model approach used by, e.g., Goss-Custard et al. (1995), Pettifor et al. (2000) and Amano et al. (2006a). All geese are assumed to have complete knowledge about the profitability of all fields within the radius geese normally forage (5 km from roost sites, details in Section 2.1 of Section 2). In order to maximise their fuelling rates, the geese move between the fields that offer the highest intake of metabolisable energy (ME). Each super goose leaves the roost after civil twilight and moves to a field with highest ME within 5 km radius from that roost. If there is more than one field with the same ME value, the super goose chooses one at random. The super goose stays on this field according to field leaving rules 1–4 (Table 2).

2.4.3. Foraging decision rule 3: Asocial learning (hereafter, FDR 3-asocial learning)

This foraging decision rule assumes that geese gradually learn where the profitable fields are located, but that they do not possess perfect knowledge about the environment. This makes them return to places where they previously gained a high net energy intake (Bernstein et al., 1988; Amano et al., 2006a; Nolet et al., 2006; Nabe-Nielsen et al., 2013). We assume that individual geese only acquire information through their own experience (asocial learning), because this type of learning is optimal in a patchy and dynamic landscape (see Németh and Moore (2014) for a review about social and asocial learning). Each super goose leaves the night roost after civil twilight and goes to the field that resulted in the highest ME on the previous day. During the rest of the day, geese move similarly to FDR 1-random (Table 2). On the first day after arrival to Mid-Norway geese select a random field <5 km from the roost, because they do not yet possess any knowledge about the area. A super goose stays on the fields according to field leaving rules 1–4 (Table 2).

Table 2
Movement of geese under each foraging decision rule (FDR). ME stands from metabolisable energy.

FDR	Field leaving rule 1	Field leaving rule 2	Field leaving rule 3	Field leaving rule 4
	<i>Current gain rate < expected gain rate</i>	<i>Digestive break</i>	<i>Disturbed</i>	<i>it is getting dark</i>
1	Move to a random field within 1 km from the current location ^c	Move to a random roost within 5 km from the current field ^a , then move to a random field within 1 km from that roost	If ≤1 km from any roost ^b , move to this roost, then move to a random field within 1 km from that roost site ^c ; if >1 km from any roost, move to a random field within 1 km from the current location ^c	move to a random roost within 5 km from the current location
2	Move to a next field offering highest metabolisable energy (ME) ^{d,e}	Move to the closest roost from the current field ^a , then move to the next field with highest ME within 1 km from that roost ^{d,e}	If ≤1 km from any roost ^b , move to this roost, then move to the next field offering highest ME within 1 km from that roost site ^c ; if >1 km from any roost, move to the next field offering highest ME within 1 km from the current location ^{d,e}	move to the closest roost from the current location
3	As in FDR 1	Move to the closest roost from the current field ^a , then move to a random field within 1 km from that roost ^c	As in FDR 1	as in FDR 2
4	Move to a random field within 1 km from the current field which is already occupied by at least one super goose ^f .	Move to the closest roost from the current field ^a , then move to a random field within 1 km from this roost already occupied by at least one super goose ^f	If ≤1 km from any roost ^b , move to this roost, then move to the next, random field already occupied by at least one super goose within 1 km from that roost site ^c ; if >1 km from any roost, move to a random field within 1 km from this roost already occupied by at least one super goose ^f	as in FDR 2
5	As in FDR 4	As in FDR 4	As in FDR 4	as in FDR 2

^a Each super-geese stays on this roost 2–3 steps before moving to the next field mimicking retention time—time when food is processed in the guts (Burton et al., 1979; Demment and Van Soest, 1985). Number of steps (2 or 3) is assigned randomly to each super-geese and this assignment is done every time a super-geese visits a roost.

^b Each super-geese stays on this roost 1 step before moving to the next field.

^c If there is no field within 1 km, move to a random field within 5 km.

^d If there is no field of any type within 1 km, choose a field with highest ME within 5 km.

^e If there is more than one field with the same ME value, choose one at random.

^f If there is no field within that radius which is occupied by another individual, chose the next field at random within 1 km. If there is no field at all within 1 km, move to a random, already occupied field within 5 km or a random field if there are no other geese within that radius.

2.4.4. Foraging decision rule 4: Social learning (hereafter, FDR 4-social learning)

This foraging decision rule was developed following the idea that birds migrating in flocks rely on the experience of other members of the flock (e.g. Németh and Moore, 2007; Guttal and Couzin, 2010). Birds therefore select fields where other geese are already foraging. Geese leave the roosts after civil twilight and move to a random field where other geese (at least one more super goose) are present, <5 km from the roost. If none of the fields are already occupied, geese move to a random field within 5 km. This rule also applies at the beginning of each day, when geese leave roost sites simultaneously. Geese stay on this field according to field leaving rules 1–4 (Table 2).

2.4.5. Foraging decision rule 5: Social and asocial learning (hereafter, FDR 5-all learning)

This foraging decision rule was developed following the idea that birds living in flocks rely on knowledge and experience of other members of the flock; however, as such information may be inaccurate in a patchy and dynamic landscape (Németh and Moore, 2014), geese also acquire information through their own experience (asocial learning). Such a combination of individual gathering of information and information obtained from observing the locations and activities of others can improve the speed and accuracy with which individuals assesses habitat quality (Németh and Moore, 2007). According to this rule geese leave the night roost after civil twilight and go to the field that resulted in the highest ME the previous day as in FDR 3-asocial learning. On the first day after arrival to Mid-Norway geese leave their night roost to a random field <5 km away. Geese forage on the fields already occupied

by other geese for the rest of the day as explained for FDR 4-social learning. Geese stay on these fields according to field leaving rules 1–4 as described in Table 2.

2.5. Parameterisation

Most of the model parameters were assigned using values collected in the field, in the laboratory or in published literature (Table 1). The parameters that we had no field data for were parameterised using POM. This included time of the first passage, the distance between a field from which geese were disturbed and the closest roost, which determines whether geese move to the roost after being disturbed or to a field (termed 'roost-disturbance radius', see Section 2.4 and Table 2), and the memory factor of the geese (α) (Appendix A, Eq. (A5)). We followed the POM strategy to identify the combination of these three parameters that best reproduced the five observed patterns (see Section 2.3). These three parameters were set to the following values: time of the first passage: 1–4 h with 0.5 intervals; roost-disturbance radius: 0.1–1 km with 0.1 km intervals; alpha 0.001; 0.01; 0.03; 0.05; 0.07 and 1. We ran 10 simulations for each of the 420 parameter combinations for each FDR. We used an average value of a given output of these 10 simulations for further analysis. Following Frank and Baret (2013), we used the sum of standardised squared errors (SSSE) to evaluate the agreement between the observed (obs) and predicted (pred) values for each FDR and each observed pattern.

$$SSSE_{k,j} = \sum_{i=1}^n \frac{(\text{pred}_i - \text{obs}_i)^2}{\text{obs}_i} \quad (2)$$

Table 3

The list of parameters and their minimum and maximum values used in the sensitivity analysis.

Parameter	Unit	Min	Max
Number of geese in a super-geese		15	25
Probability of disturbance—small fields	%	0	0.6
Probability of disturbance—large fields	%	0	0.4
Global disturbance	%	0	0.5
Additional moving north stores	kJ	−11274	11274
Additional initial stores	kJ	−4735	4735
Field size threshold	km ²	0.05	0.08
Small radius	km	0.75	1.25

Here k is each FDR, j each of the five observed patterns and i is each day of simulation. The foraging decision rule which best fit a given observed pattern was indicated by the lowest SSSE value. Next, we followed a Monte Carlo Filtering approach, by which tested patterns were applied as filters to separate good from bad sets of parameter values (Wiegand et al., 2003; Grimm and Railsback, 2005). To do this, quantitative criteria for the agreement between observed and predicted patterns were developed. The observed patterns were ranked from the most to least important as presented in section Section 2.3. Pattern 1 (daily net energy intake; DNEI) was used as the first filter. We only retained the parameter sets which reproduced the observed DNEI $\pm 10\%$. We therefore considered an observed DNEI pattern to be accurately reproduced by a model simulation when SSSE was within $\pm 10\%$ of the mean observed DNEI for four periods. Second, from this reduced set, we identified parameter combinations that allowed us to reproduce pattern 2 (time spent on roost sites) within 10% of the mean values observed in the field for all four periods. Finally, we repeated the same procedure, retaining parameter sets that allowed the model to reproduce patterns 3–5, one pattern at a time. The SSSE value can be artificially reduced when observed or predicted data show little or no variation (Duriez et al., 2009). It was thus complemented by a visual inspection of the fit between observed and predicted data. We performed this filtering approach for each FDR separately. From the final sets of parameters for each FDR, we only chose this set which was common for all five FDRs. This led to one set of parameters with time of the first passage = 3 h; roost-disturbance radius = 1 km and $\alpha = 0.07$ (Table 1). After identification of FDR that best reproduced all five observed pattern, we performed additional parameterisation with the same method as described above in order to check whether different set of the three parameters would result in a better fit between the observed patterns and the model outcome of this FDR.

2.6. Sensitivity analyses

Although we used empirically collected and literature-based values to build the model, we performed a global sensitivity analysis to evaluate how the patterns emerging from the model were affected by variations in the input parameters. The aim was to decompose the model outputs' variance into variances attributable to each input parameter, but also to evaluate the interaction between parameters. We ran the sensitivity analysis only on FDRs that best described the behaviour of geese and applied the variance decomposition technique as suggested by Sobol' (1990), see the review by Thiele et al. (2014) for summary on sensitivity analysis. We started by defining the list with values of each parameters used in the sensitivity analysis and with all the possible combinations of these values, which were later used to run the simulations of the given FDRs. The model sensitivity was analysed for parameter values $\pm 25\%$ from the values used in the final simulations of FDRs (Tables 1 and 3). We also wanted to test the robustness of the model to disturbance *per se* and therefore on top of the $\pm 25\%$

variation in disturbance probability, we added situations where disturbance on small or large fields was increased or decreased by 100% (so called 'Global disturbance'). We ran one simulation with parameters' combination for each FDR. We used the *sensitivity* R package (Pujol et al., 2014) using the formulas by Jansen (1999) and Saltelli et al. (2010) to define the final list of parameter combination and to run the rest of the sensitivity analysis. The Jansen formula (sobeljansen formula in *sensitivity* R package) implements the Monte Carlo estimation of the Sobol indices for both first-order and total indices at the same time. Sobol's first order sensitivity indices (S_i) measure the effect of varying a focus parameter alone, but averaged over variations in other input parameters, thus providing information on the average reduction of output variance when the parameter is fixed. Sobol's total effect sensitivity indices (S_{Ti}) measure the contribution to the output variance of the focus parameter, including all variance caused by its interactions, of any order, with any other input parameters. The number of tested settings was given by $m \times (p + 2)$, where m is the size of the Monte Carlo sample matrix ($m = 400$ in this study) and p is the number of parameters to analyse ($p = 8$ in this study, Table 3). This led to 4000 model runs. In order to assess the sensitivity of the FDRs predictions to the values of parameter estimates, we investigated the changes in daily net energy intake (pattern 1) and proportion of daytime spent on roost sites (pattern 2).

2.7. Statistical analyses used for evaluation of emergent patterns based on pattern-oriented modelling approach

To find out which foraging decision rule best match with all the observed patterns, we used the SSSE as described in Section 2.5. For pattern 3 (spatiotemporal distribution of geese) we only used visual inspection. The foraging decision rule which had the lowest SSSE for the largest number of patterns was considered best describing the foraging behaviour of geese.

In order to compare changes in DNEI between periods for different FDRs we used ANOVA if there was no evidence of any significant difference in variance across the output values based on the models' simulations, tested with the use of the Fligner–Killeen test of homogeneity of variance (Conover et al., 2011). Otherwise, we used one-way test with Welch's correction for variance non-homogeneity (henceforth referred to as one-way; Welch, 1951). The same tests were applied to analyse the diurnal and in-between period changes in the spatial distribution of geese. We used visual inspection to test for normality of model residuals (Quinn and Keough, 2002; Zuur et al., 2007). Both residuals of DNEI and the diurnal and in-between period changes in the spatial distribution of geese were normally distributed. All statistical analyses were performed in R 3.1.0 (R Development Core Team, 2013). Results are shown as mean \pm SD unless otherwise indicated. The significance level was set to $p < 0.05$ for all statistical tests.

3. Results

3.1. Comparison of the predictions of the five foraging decision rules

We analysed the ability of the five foraging decision rules to reproduce the five different patterns observed for field data:

3.1.1. Pattern 1—Daily net energy intake

In the FDR 1-random and FDR 4-social learning geese obtained lower daily net energy intake (DNEI) than observed in the field for all four periods. Predictions of DNEI under FDR 2-max energy and FDR 5-all learning were higher than observed in all periods. Geese gained on average 4.12 times as much energy as observed when foraging according to FDR 2-max energy (Fig. 3A). For FDR 3-asocial

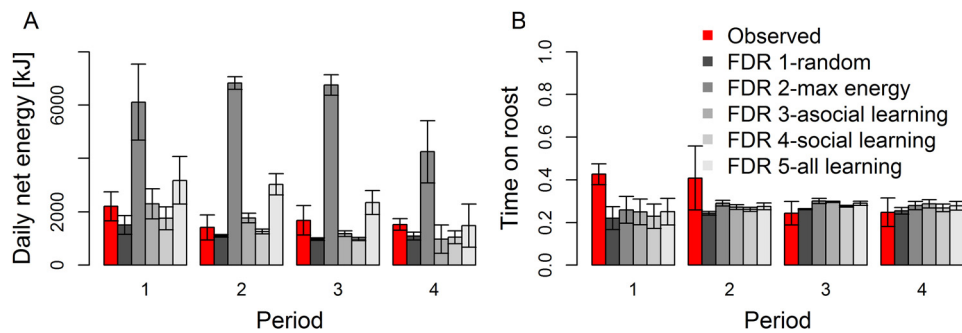


Fig. 3. Observed and predicted in-between-periods changes in daily net energy intake (A) and proportion of daylight spent on roost sites (B) for pink-footed geese at Mid-Norway spring stopover site for five foraging decision rules (FDR). Error bars in A and B for FDR predictions show \pm SD from 100 replicates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

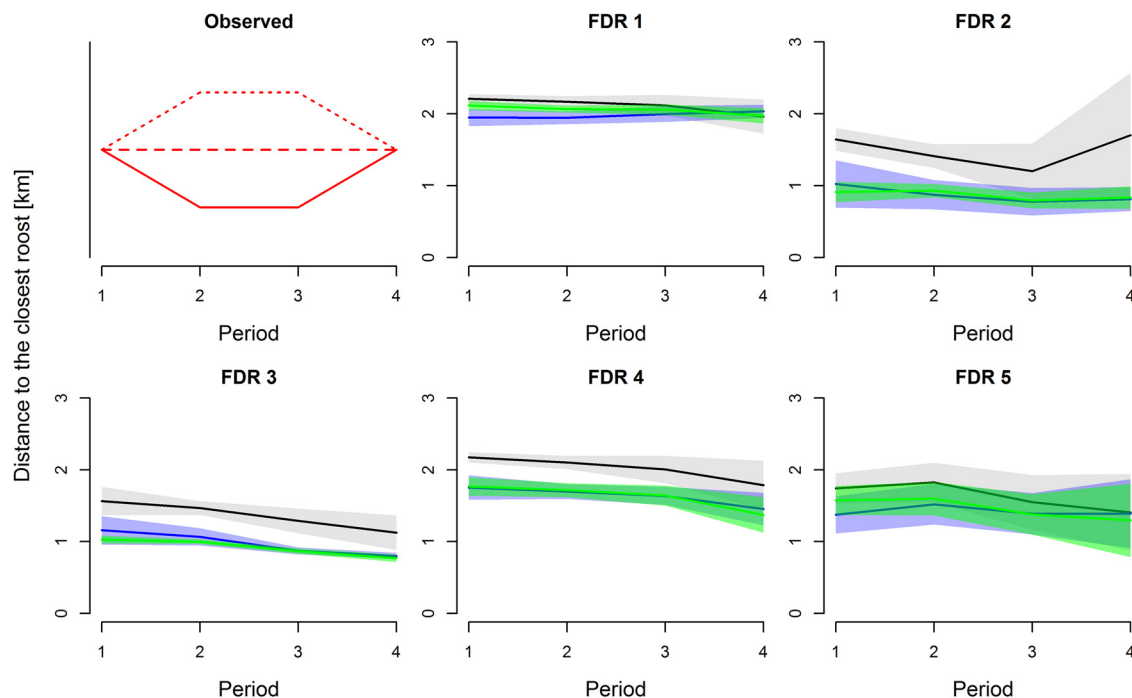


Fig. 4. Diurnal and in-between-periods changes in spatiotemporal distribution of pink-footed geese staging in Mid-Norway in relation to the closest roost site predicted for each foraging decision rule (FDR). Solid lines represent the average of 100 replicates: **black-morning** (05:00–11:00), **blue-midday** (11:00–16:00), **green-evening** (16:00–21:00). The shaded areas in matching colours around each line show \pm SD from 100 replicates. The red lines show the observed changes in goose distribution based on the habitat selection analyses with the use of Resource Selection Function (RSF). The results of RSF are relative values in geese's distances to the roost hence the observed distribution is schematic with no values on the y-axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

learning the predicted DNEI was closer to the observed values than the other four FDRs, especially in the first two periods (mean \pm SD observed and predicted under FDR 3-asocial learning values of DNEI respectively: 1706 ± 445 kJ day⁻¹; 1556 ± 600 kJ day⁻¹) (Fig. 3A). This FDR had the lowest SSSE value (Fig. 7). The values of DNEI predicted by FDRs 2 and 5 were the least accordant with the observed values (Figs. 3A and 7). The predictions of FDR 3-asocial learning showed no between-period difference in DNEI (ANOVA: $F_{3,39} = 1.08$, $p = 0.38$) which is in agreement with the observed pattern. The remaining four FDRs showed between-period difference in DNEI (ANOVA: $F_{3,39} = 3.35, 8.92, 22.53, 20.67$ respectively for FDRs 1, 2, 4 and 5; $p < 0.001$ for all four FDRs).

3.1.2. Pattern 2 Time spent on roost sites

In periods 1 and 2 geese spent less time on roost sites during daytime under all five FDRs than observed, but for periods 3 and 4 predictions of all five FDRs were comparable to the observed values

(Fig. 3B). FDR 3-asocial learning had the lowest SSSE value among all FDRs for that pattern (Fig. 7)

3.1.3. Pattern 3—Spatiotemporal distribution of geese

None of the FDR accurately predicted the spatiotemporal changes in distribution of pink-footed geese (Fig. 4). Predictions of FDR 1-random showed no statistically significant spatiotemporal changes in goose distribution relative to roost sites during the day (Table 4, Fig. 4), which is in accordance with observations from periods 1 and 4 and contrary to observation from periods 2 and 3. FDRs 2–4 predicted differences in the goose distribution both during the day and in-between the periods; however, the differences did not match the observed pattern (Table 4, Fig. 4). Predictions of FDR 5-all learning show changes in goose distribution in the first half of the stopover season (periods 1 and 2) and no changes in the second half (periods 3 and 4; Table 4, Fig. 4).

Table 4

The results of Fligner–Killeen test of homogeneity of variance (Variance), ANOVA and one-way test with Welch's corrections for variance homogeneity (one-way) testing statistical differences in diurnal and in-between periods changes in spatiotemporal distribution of pink-footed geese in relation to the closest roost site in Mid-Norway predicted for the five foraging decision rules (FDR). If the results of the Fligner–Killeen test did not indicate a significant difference in variance across the results from different time of day (if $p > 0.05$, Variance = N), we performed ANOVA on such results. Otherwise ($p \leq 0.05$, Variance = Y), we used one-way test.

FDR	Period	Variance	ANOVA (df=2, res=297)		One-way	
			F	p	F	p
1	1	Y			11.3	0.06
	2	N	13.6	0.08		
	3	N	9.4	0.12		
	4	Y			11.7	0.06
2	1	N	5448	<0.001		
	2	N	5759	<0.001		
	3	Y			1259.6	<0.001
	4	Y			2234.9	<0.001
3	1	Y			14315	<0.001
	2	Y			13694	<0.001
	3	Y			15735	<0.001
	4	Y			9003	<0.001
4	1	Y			10119.9	<0.001
	2	Y			7639.3	<0.001
	3	Y			4135.6	<0.001
	4	Y			1442.1	<0.001
5	1	N	996	<0.001		
	2	N	218.9	<0.001		
	3	N	16.2	0.05		
	4	N	13.1	0.08		

3.1.4. Pattern 4—Phenology

For all FDRs almost all geese (92, 96, 97, 94 and 99%, respectively) migrated north by the end of simulations as observed in the field and the predicted phenology resembled the observed one (Fig. 5). The SSSE was lowest for FDR 1-random (Fig. 7). There was not more than 1 super goose starving in any of the simulations.

3.1.5. Pattern 5—Distribution on roost sites

The observed and predicted maximum number of geese on different roost sites agreed well for several FDRs (Fig. 6), but the correspondence was best for FDR 3-asocial learning (Fig. 7). There was no significant correlation between observed and predicted numbers for any of the FDRs (Pearson's correlation (p values for all FDRs > 0.1 , r for each FDR = -0.34 , -0.19 , -0.01 , -0.21 and -0.20) indicating that the ability of each FDR to reproduce the observed pattern was not related to the number of observed geese.

The study area is only part of Mid-Norway and in reality pink-footed geese also forage in areas outside the study site. The number of geese on roost sites observed in the real world may therefore be influenced by foraging areas not included in the study area, and this effect may be most pronounced at the roost sites located at the edge of the modelled area ('edge effect'). The simulated numbers may therefore not match the observed values at the edges of the study site due to reasons other than processes included in the model. We tested for the edge effect by fitting a generalised additive model (GAM) using a non-parametric smoother with the predicted values of each FDR as a response and the observed values and latitude and longitude of each roost site as predictors. Only FDR 1-random showed the 'edge effect' both along latitude and longitude axis ($F_{\text{lat}} = 31.9$, $p_{\text{lat}} < 0.01$; $F_{\text{long}} = 8.1$ and $p_{\text{long}} = 0.007$).

3.2. Summary of results

FDR 3-asocial learning had the lowest difference between the simulated and observed patterns (as measured with SSSE) for three out of five patterns (Fig. 7), including patterns 1 and 2, which

we consider the most important ones. FDR 1-random best predicted pattern 3 describing changes in spatiotemporal distribution of geese and resulted in the lowest SSSE for pattern 4 (phenology of geese).

3.3. Sensitivity analysis and post-result parameterisation

Here we present the results of sensitivity analysis on FDR 3-asocial learning, as this FDR best described the foraging behaviour of pink-footed geese. However, the predictions of FDR 1-random were more accurate than FDR 3-asocial learning for two patterns; and therefore we present the sensitivity analysis for that FDR in Appendix B.

For FDR 3-asocial learning, the average DNEI over the four periods varied between 497 and 2620.8 kJ day^{-1} (mean \pm SD: $1350 \pm 458.9 \text{ kJ day}^{-1}$). This range is $\pm 68\%$ of the average value estimated by FDR 3-asocial learning with the use of final parameter settings ($1555.6 \text{ kJ day}^{-1}$). The sum of main effect indices, S_i was 0.96. A value close to 1 that indicates that the model is almost purely additive, i.e. there is a negligible interaction between parameters, with a strong contribution of the main effect of probability of disturbance on large fields (responsible for 41.3% of the variation of the DNEI, Fig. 8) and simultaneous changes of the probability of disturbance on all fields ('Global disturbance'; 57.7% of the variance, Fig. 8). When the probability of disturbance on all fields ('Global disturbance') was increased by approximately 100%, the mean DNEI for all four periods decreased by 60% in comparison to DNEI estimated by FDR 3-asocial learning (with the use of the final parameter settings). Simulations with almost no disturbance in FDR 3-asocial learning resulted in an increase of the mean DNEI over the four periods by 52% in comparison to DNEI estimated by FDR 3-asocial learning.

The variation in time spent on roost sites during daytime was smaller than the variation in DNEI (22–28% of daytime, mean \pm SD: $26 \pm 1\%$; ± 0 –21% of the average time geese spent on roost during daytime estimated by FDR 3-asocial learning (28%)). The sum of S_i was 0.82, indicating that the model is largely additive. The distance that geese move between different fields ('small

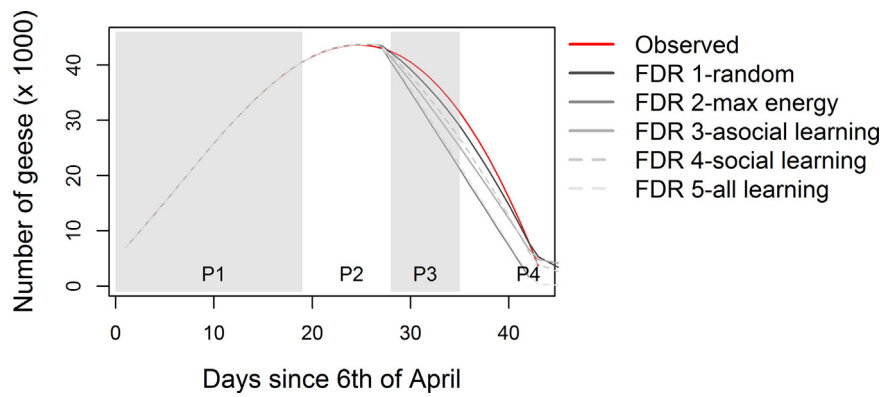


Fig. 5. Observed and predicted in-between-periods changes in number of pink-footed geese at Mid-Norway spring stopover site for five foraging decision rules (FDR). Shaded areas indicate duration of each period (P–P4). The SD for each FDR predictions fall within $\pm 2\%$ of the mean value and are therefore not shown in the graph. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

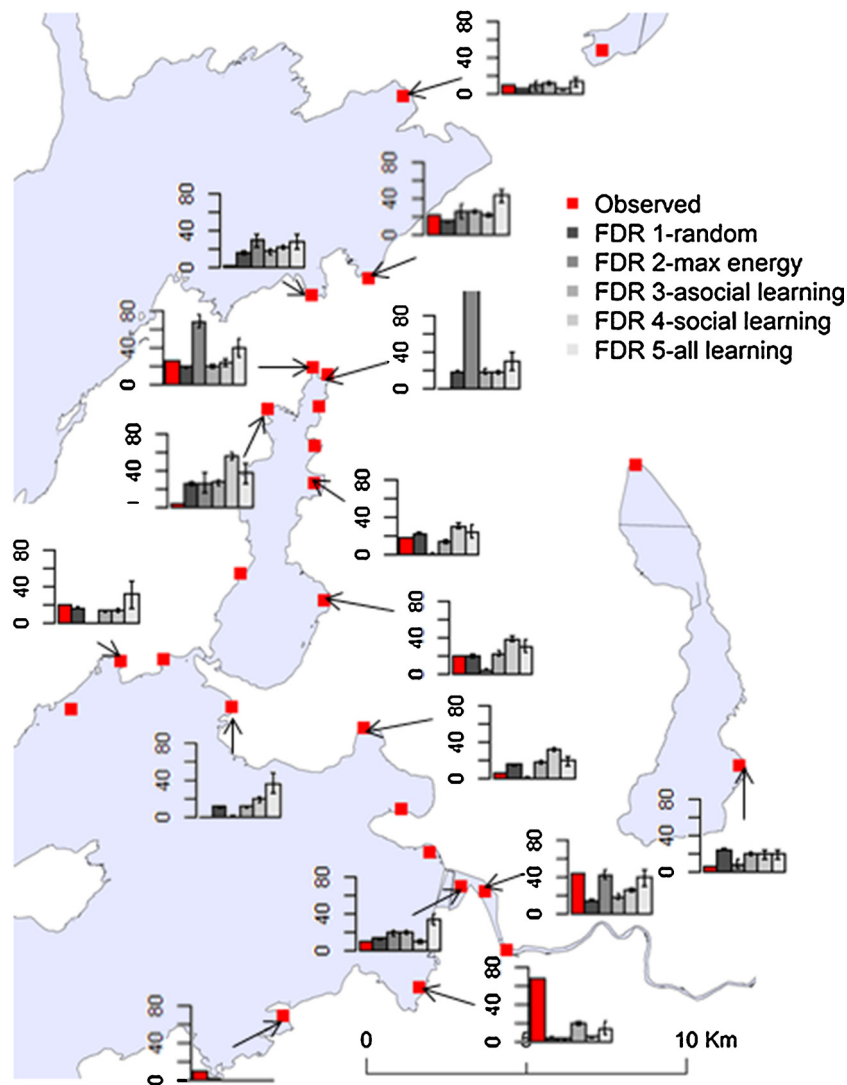


Fig. 6. Observed and predicted number of pink-footed geese on different roost sites. Observed maximum numbers over the entire stopover season (red) are compared with predictions for five different foraging decision rules (FDR). Error bars for FDR predictions show \pm SD from 100 replicates. The y-axis of each graph shows number of geese multiplied by 100. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

displacement radius') was responsible for almost the entire variation in the output (95%, Fig. 8). When geese were allowed to move only short distances between fields (≤ 0.8 km) they spent more time on the roost sites (26–28% of daytime), whereas a larger value

(≥ 1.1 km) caused them to spend between 22–26% of the daytime on roosts. The values of S_i and S_{Ti} are similar for most parameters. There are only small differences between these two indices for probability of disturbance on large fields, global disturbance

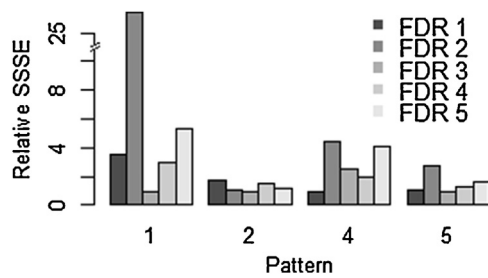


Fig. 7. The sum of standardised squared errors (SSSE) between observed and predicted values for each foraging decision rule (FDR) for four tested patterns (1—daily net energy intake, 2—proportion of daylight spent on roost sites, 4—phenology of geese and 5—distribution of geese among roost sites in Mid-Norway). Relative SSSE represents SSSE values divided by the value of FDR with the lowest SSSE for each specific pattern. Note the break in the y-axis. The fit of the simulated values for pattern 3—spatiotemporal distribution of geese in respect to the closest roost site was only evaluated based on the visual inspection of the results.

and small displacement radius (Fig. 8), indicating weak interactions among them. Changes in global disturbance had a small effect on the amount of time geese spent on roost sites during daytime; the mean value over four periods for the models with increased or decreased disturbance was equal to the mean value for all simulations and was equal to 26%.

The post-result parameterisation of FDR 3-random revealed that two sets of parameters resulted in the best, identical, fit between the observed patterns and the model outcome of this FDR. The first set was identical to the one established by the initial parameterisation (time of the first passage = 3 h; roost-disturbance radius = 1 km and $\alpha = 0.07$); the second was comparable (time of the first passage = 3 h; roost-disturbance radius = 1 km and $\alpha = 0.05$). The final results are shown with the first set.

4. Discussion

In this study we used an individual-based model to study foraging decision of pink-footed geese during their spring migration. Our results suggest that while studied geese employ a random search strategy, they are also able to learn based on their own experience where the most profitable patches are located and return to the patches that resulted in highest energy intake.

These findings are likely influenced by the overall high quality of the food resources available in the Mid-Norway landscape, as grain (in stubble fields and new-sown fields) is a good source of

energy and grass is rich in protein (Prop and Spaans, 2004). When resources are abundant across the landscape, choosing one forage resource over the other does not provide much benefit in terms of nutrient intake. In this situation random search will be close to optimal (Turner et al., 1993). Resource selection function analysis also revealed that pink-footed geese in Mid-Norway choose resources according to their availability, and therefore select fields at random (Chudzińska et al., 2015). Furthermore, the geese are foraging in a highly dynamic agricultural landscape where the food type on a given field may change within a relatively short time. In such a landscape, where individuals are unlikely to have sufficient knowledge about the environment (as also revealed by the results of FDR 2-max energy), choosing patches at random may be more beneficial than returning to a patch visited few days before, as this may reduce search time and energy expenditure (Amano et al., 2006a,b). The Mid-Norway staging site is a relatively large area ($50 \times 30 \text{ km}^2$) and habitat depletion and disappearance/appearance occur simultaneously in various places because of foraging and agricultural practices. On top of that, both variability in grain density on stubble fields and the fact that grain on new sown fields is sown at varying depths, from the surface to several centimetres below (Madsen, 1985b), hinder the assessment of the profitability of these field types without landing there. This makes it difficult for the geese to obtain a complete knowledge about the spatial distribution of food and choosing fields according to their availability (random) seems more beneficial. Similar random choice of foraging habitat has been found for other species living in highly dynamic landscapes (Focardi et al., 1996; Kułakowska et al., 2014). Outside spring migration season geese, however, have been reported showing selection for certain habitat types mainly based on nutritional values of these habitats (Newton and Campbell, 1970; Owen, 1973; McKay et al., 1996).

FDR 3-asocial learning reproduced most of the observed patterns including patterns describing daily energy intake and time spend on roost sites, the most important ones. Returning to a recently visited patch can be beneficial because in the agricultural landscape the probability that the resource type on such a patch remains the same as one day before is higher than if the same patch is visited after longer period of time. Several studies have shown that animals may return to the same area to forage if they experienced suitable foraging conditions at that area (e.g., Charnov, 1976; Bailey, 1995; Bailey et al., 1996). Bernstein et al. (1988) revealed that incompletely informed foragers selecting patches randomly could distribute themselves optimally by learning habitat quality and using a patch departure rule based on the

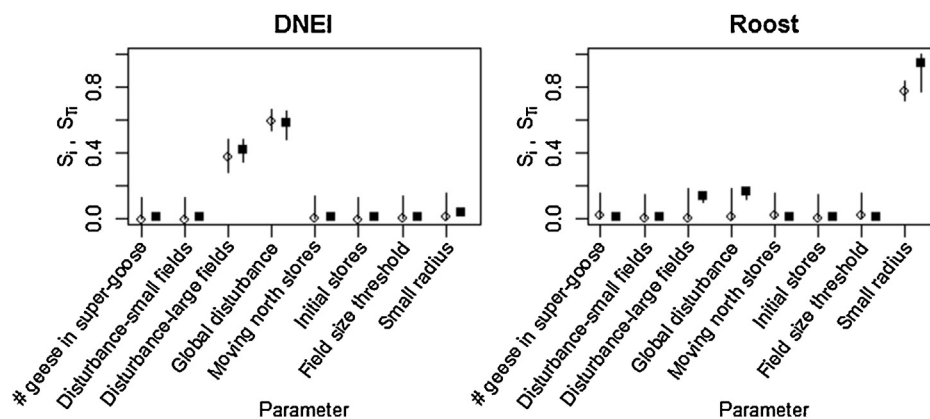


Fig. 8. Results of the sensitivity analysis based on Sobol' method for the two patterns: pattern 1—daily net energy intake (DNEI) and pattern 2—time geese spend on roost during daylight (roost) for foraging decision rule 3 (asocial learning), which best described foraging behaviour of pink-footed geese during their spring-staging stopover site in Mid-Norway. Open circles show first-order sensitivity index values (S_1), i.e., main effects. Black squares show total sensitivity index values (S_{11}), i.e., total (main and all interaction) effects. Bars show bootstrapped 95% confidence intervals of corresponding sensitivity indices.

marginal value theorem (Charnov, 1976) as is the case in this study. Models including social learning (FDRs 4 and 5) led to less realistic energy intake rates and spatial distributions of geese. This contrasts other studies demonstrating benefits of group foraging for geese and other species (Amano et al., 2006a; Németh and Moore, 2007; Kułakowska et al., 2014). In our model, one agent consisted of 20 individuals. Our model does not rule out the benefits of geese foraging in small flocks but indicates that foraging in larger flocks may not be beneficial. This is likely to be influenced by the fact that due to a large number of pink-footed geese foraging at the study site (approx. 80,000 individuals, Madsen and Williams, 2012), large flocks concentrated on a small patch would lead to a fast habitat depletion, and it is therefore more beneficial for geese to forage in more wide-spread and small flocks. Although socially gathered information regarding location of profitable foraging areas may not be a primary type of information exchanged between individuals from the same flock, other exchange of information, like optimal time of departure from a stopover site, can still take place. Most studies focusing on species frequently living in flocks often point out the benefits of social learning (Rafacz and Templeton, 2003; Amano et al., 2006a; Németh and Moore, 2007; Kułakowska et al., 2014); however, our study also revealed the relevance of asocial learning for such species. Although detailed analysis of how such learning is accomplished by geese and which cues are crucial in this process was not the aim of this work, this is an interesting aspect worth further analysis.

The sensitivity analysis revealed the pervasive role of human disturbance on foraging behaviour of pink-footed geese in Mid-Norway. Indeed, the behaviour of pink-footed geese at this stopover site, as well as at other stopover sites along the migration route, is known to be strongly influenced by disturbance (Madsen, 1994, 1998; Klaassen et al., 2006; Jensen et al., 2008; Chudzińska et al., 2013). Other goose species are also known to be susceptible to human disturbance (Owen, 1973; Madsen, 1994; Stillman et al., 2015). The foraging behaviour of pink-footed geese in Mid-Norway is influenced by various types of disturbances, some of which are predictable, such as regular road traffic, while others are more unpredictable, such as farming activities or irregular passage of walking people. The type of disturbance influences for how long geese forage and their habitat selection (Chudzińska et al., 2013, 2015). The difference between the results of the sensitivity analysis of pattern 2 (time spent on roost sites) of FDR 1-random and FDR 3-asocial learning may indicate that the location of high quality areas in relation to the closest roost sites may determine goose behaviour, in agreement with previous studies (Jensen et al., 2008; Chudzińska et al., 2013, 2015).

Although IBMs can be powerful tools for analysing whether different behavioural mechanisms can lead to realistic emergent properties, they have often been criticised for being too complex or too simple and data deficient, making it difficult to test their validity (Grimm et al., 1999; Grimm and Railsback, 2005; Evans et al., 2013). In the following paragraphs we discuss how our model can be improved by adding or modifying some aspects of foraging behaviour of the studied geese. None of the predictions of the FDRs were in agreement with the observed pattern describing the proportion of daytime geese spent on roost sites for the first two periods of the stopover season. A study based on GPS-tagged pink-footed geese revealed that in Mid-Norway geese spent more time on roost sites than necessary for digestion, and human disturbance was suggested as the main reason why geese returned to roost sites during a day (Chudzińska, unpubl. manuscript), although little is known about the mechanism that drives such behaviour. In the beginning of the stopover season, geese may not be familiar with factors causing disturbance and hence spend longer time on roost sites than at the end of the season when they may have learned how to avoid or habituate to disturbances. Such adaptive behaviour has

not been included in the model and more information, preferably experimental, should be gathered.

None of the predictions of the FDRs were able to accurately mimic how the distance between the foraging patch used by geese and the roost sites changed along the day and between periods. The spatiotemporal distribution of geese can be influenced by many factors, several of which are not included in the current design of the model. Geese may explore patches in the vicinity of their current patch and only when these patches are depleted, move to another area. In the current design of FDR 3-asocial learning and FDR 5-all learning, geese only return to the previously visited patch once per day in the morning but the search rule thenceforth is random (FDR 3-asocial learning) or depends on the distribution of other geese (FDR 5-all learning). In our model, geese leave a patch not only based on their energy intake on that patch but also due to physiological and external factors (disturbance, time of day). We do not include any form of adaptation or additional learning in our model and therefore geese do not return to a recently abandoned patch (e.g. neither the foraging patch that resulted in high energy intake, nor a patch where they experienced low disturbance level) at any time of day other than in the morning, unless they do so by chance. The analysis of how the studied species selected foraging habitats using resource selection functions revealed that spatiotemporal changes in the goose distribution relative to the roost sites are largely shaped by density-dependent processes (Chudzińska et al., 2015). Such processes are represented in our model through habitat depletion by other individuals (exploitative competition) and through a relationship between number of animals and the amount of time they spend foraging and being vigilant. However, other competitive processes, such as the behavioural responses induced by aggressive interactions (interference) that may limit the maximum number of geese occupying a certain space, are not included. More empirical studies about site fidelity of geese, density-dependent processes and the adaptation by geese to disturbance are necessary.

The model presented in this study has a potential for both theoretical and practical applications. It revealed that pink-footed geese do not follow the foraging models most commonly proposed for migrating capital breeders, which assume maximising energy intake. Instead, foraging decisions of such migrants are based on their experience and habitat availability and are influenced by the amount of information they possess during foraging and mode of obtaining such information. Most likely, an optimal foraging strategy is site and species-specific. For example, for woodpigeons (*Columbus palumbus*), which only migrate locally and forage on a dynamic agricultural landscape, the most optimal foraging strategy was to join other conspecific as well as rely on own experience; however, random selection of available resources was also optimal at certain circumstances (Kułakowska et al., 2014). White-fronted geese (*Anser albifrons*) foraging during their spring migration in Japan in an area dominated by one food source also benefited from group foraging (Amano et al., 2006a). For capital breeders foraging during spring migration at a stopover site where habitat availability is very dynamic and there is high intraspecific competition for resources due to large number of individuals foraging at the same time in a limited space and time, foraging at random and relying on own experience seems to be the most beneficial option. Such conditions may apply for example to most migrating European geese. These populations are currently increasing and are frequently observed foraging on agricultural fields during spring migration (Fox et al., 2005, 2010) as well as other migratory bird species gathering in large numbers at distinct stopover sites. Although our model is highly specific and tied to data from a long-term field study in a specific area, the insights into the relevance of learning processes and optimal foraging provide general building blocks for representing adaptive behaviour in dynamic

environments (Railsback and Harvey, 2002; Grimm and Railsback, 2012).

The presented model has a potential for risk assessment where information about spatial and temporal aspects of foraging and/or the effect of various external factor on energetics are necessary. Due to the fact that the Svalbard-breeding population of pink-footed geese has increased dramatically in the last decade (Madsen and Williams, 2012), the conflict between agricultural owners and geese foraging on their fields increased and led to an agricultural subsidy scheme to alleviate this conflict (Tombre et al., 2013). Because geese are allowed to forage undisturbed at the subsidised fields, geese are frequently chased away at remaining areas in order to reduce their damage to crops. Our model, which incorporates human disturbance, can be applied to predict the population-level and energetic consequences of, for example, increased scaring intensity or concentration of such scaring in certain areas. Our results suggest that when the probability of disturbance on all fields was increased by approximately 100%, the mean DNEI for all four periods decreased by 60%. Our model can be used to predict the consequences of different management scenarios and thus help solve critical practical questions, such as: can the effect of disturbance on geese be reduced if disturbance varies temporally and/or spatially? Our model also demonstrated that pink-footed geese staging in Mid-Norway may not benefit from foraging in large flocks. It can therefore be used to support decision making regarding the definition of management schemes of protected or subsidised areas by providing key information, for example, about how big the areas should be and how close to each other they should be placed. Our model can also be used to predict the effect of changes in habitat availability and alternative agricultural practices in Mid-Norway on population dynamics, revealing the optimal policies with regard to when to plough and re-sow fields to reduce agricultural conflicts and/or potential effects of introduction of new crop types such as winter wheat.

We thus believe that our and similar models (e.g. Kułakowska et al., 2014; Stillman et al., 2015), which are based on individual behaviour and energetics, can be valuable tools for making more realistic and ecologically relevant risk assessments of human disturbance and changes in agricultural practices.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2015.10.005>.

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