

Oikos 124: 851–860, 2015

doi: 10.1111/oik.01881

© 2015 The Authors. This an Online Open article

Subject Editor: Rob Robinson. Editor-in-Chief: Dries Bonte. Accepted 1 December 2014

Using habitat selection theories to predict the spatiotemporal distribution of migratory birds during stopover – a case study of pink-footed geese *Anser brachyrhynchus*

Magda E. Chudzińska, Floris M. van Beest, Jesper Madsen and Jacob Nabe-Nielsen

M. E. Chudzińska (chudzinskam@gmail.com), F. M. van Beest and J. Nabe-Nielsen, Dept of Bioscience, Aarhus Univ., Frederiksborgvej 399, DK-4000 Roskilde, Denmark. – J. Madsen, Dept of Bioscience, Aarhus Univ., Grenåvej 14, DK-8410 Ronde, Denmark.

Understanding how animals select for habitat and foraging resources therein is a crucial component of basic and applied ecology. The selection process is typically influenced by a variety of environmental conditions including the spatial and temporal variation in the quantity and quality of food resources, predation or disturbance risks, and inter- and intraspecific competition. Indeed, some of the most commonly employed ecological theories used to describe how animals choose foraging sites are: nutrient intake maximisation, density-dependent habitat selection, central-place foraging, and predation risk effects. Even though these theories are not mutually exclusive, rarely are multiple theoretical models considered concomitantly to assess which theory, or combination thereof, best predicts observed changes in habitat selection over space and time. Here, we tested which of the above theories best-predicted habitat selection of Svalbard-breeding pink-footed geese at their main spring migration stopover site in mid-Norway by computing a series of resource selection functions (RSFs) and their predictive ability (k -fold cross validation scores). At this stopover site geese fuel intensively as a preparation for breeding and further migration. We found that the predation risk model and a combination of the density-dependent and central-place foraging models best-predicted habitat selection during stopover as geese selected for larger fields where predation risk is typically lower and selection for foraging sites changed as a function of both distance to the roost site (i.e. central-place) and changes in local density. In contrast to many other studies, the nutritional value of the available food resources did not appear to be a major limiting factor as geese used different food resources proportional to their availability. Our study shows that in an agricultural landscape where nutritional value of food resources is homogeneously high and resource availability changes rapidly; foraging behaviour of geese is largely a tradeoff between fast refuelling and disturbance/predator avoidance.

Arctic-nesting birds have a limited time to prepare for breeding as the time window when conditions are suitable for migration and for breeding is often narrow (Alerstam and Lindström 1990, Prop and Black 1998, Drent et al. 2003). Birds must accumulate fat to fuel their migration and breeding activities as well as protein to gain muscle strength and produce eggs (McDonald et al. 1973, Robbins 1993). A common migration strategy is to build up and maintain sufficient nutritional reserves (protein and fat) by foraging on stopover sites in order to arrive at the breeding areas in near-optimal breeding condition – a strategy termed capital breeding (Drent et al. 1978, Klaassen et al. 2006, Stephens et al. 2014). In most heterogeneous landscapes, however, the availability and quality of food resources varies both spatially and temporally. Besides the nutritional content of the available food resources, other factors such as

the costs related to searching and movement, predation or disturbance risk, and inter- and intraspecific competition can also greatly influence the spatiotemporal distribution of species (Sih 1980, Amano et al. 2006a, Sunde and Redpath 2006, van Beest et al. 2014). This process, termed habitat selection, is thus the outcome of tradeoffs between the costs and benefits in selecting certain foraging sites over others (Myrsterud and Ims 1998, Godvik et al. 2009).

To explain how tradeoffs in habitat selection of animals emerge, observed patterns are often tested against predictions derived from a specific theoretical model. The most commonly employed theories within a habitat selection framework are: maximising nutrient intake (Lindström 1991, Hedenström and Alerstam 1997), density-dependent habitat selection (Rosenzweig 1981, Shochat et al. 2002, McLoughlin et al. 2010), central-place foraging (Orians and Pearson 1979, Rosenberg and McKelvey 1999, van Gils and Tijssen 2007), and predation risk effects (Lima and Dill 1990, Lindström 1990, Creel et al. 2005). Although not mutually exclusive, rarely are multiple theories considered simultaneously to evaluate which framework, or combinations

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

of frameworks, best predict the observed habitat selection patterns of the study species. However, such tests are important as accurately predicting habitat selection patterns is a prerequisite for effective management and conservation of species (Boyce and McDonald 1999).

For birds migrating in steps, such as pink-footed geese *Anser brachyrhynchus*, stopover sites along the migration route are used shortly (in comparison to e.g. wintering areas) but intensively (Madsen et al. 1999). Based on a simple maximising rule, geese would be expected to focus their habitat selection purely on food resources that provide the greatest energy/protein return. However, many individual geese typically use stopover sites at the same time. As such, density related processes, such as intraspecific resource competition, could seriously affect the habitat selection process. Following density-dependent habitat selection theory, selection for high quality resources should be strongest during periods of low intraspecific competition (e.g. when the first geese arrive at stopover sites) while the strength of selection for quality resources should weaken as intraspecific competition increases (e.g. as more geese arrive at the stopover site) (McLoughlin et al. 2010, van Beest et al. 2014).

A special case of the general optimal foraging theory is the central-place foraging theory. This framework may be especially valuable to explain habitat selection patterns of geese at stopover sites as they frequently congregate at roosting areas during night and some periods of the day to rest and digest. A typical feature of central-place foraging is a declining probability of use of sites at increasing distance from the focal point (Rosenberg and McKelvey 1999). Moreover, classic central-place foragers are expected to show no distinct selection for food resources close to the focal point (where competition for food is greatest and resource depletion most likely) and increase selection of high-quality food resources as the

distance from the central-place increases (Schoener 1979). When applying this theory to a setting where local density changes rapidly but predictably (as for roosting birds at migratory stopover sites) animals should alter selection based on both the distance from the focal point (roost site) as well as temporal changes in the number of conspecifics present.

Besides the nutritional value of a site and the number of conspecifics competing for the same food resources around a central-place, predation risk and disturbance pressures within the landscape can also be crucial drivers of habitat selection (Manly et al. 1993, Madsen 1994). Indeed, minimising predation risk is considered an important determinant of behaviour of migratory birds (Hedenström and Alerstam 1997, Weber et al. 1998, Jonker et al. 2010, Chudzińska et al. 2013). Increased disturbance or predation risk may force individuals to increase selection of marginal habitat with reduced forage but greater cover or alternatively to congregate at larger fields where predators are more easily detected (Amano et al. 2006a).

In this study we quantified population-level habitat selection of pink-footed geese at their major spring-migration stopover site in mid-Norway. Our aim was to evaluate which of the aforementioned theories, or a combination thereof (Table 1), best predicted the spatial distribution of pink-footed geese at their stopover site in mid-Norway as quantified by a series of resource selection functions (RSFs).

Material and methods

Study population and site

The Svalbard-breeding population of pink-footed geese overwinters in Belgium, the Netherlands and Denmark. During

Table 1. An overview of the considered resource selection function (RSF) models with the corresponding predictor variables and predictions for habitat selection of pink-footed geese at the spring migration stopover site in mid-Norway.

Models and the used parameters	Predictions
Maximising nutrient intake	
Food resources	Geese select strongest for food resources with the highest nutritional value
Density-dependent habitat selection (DD)	
Time	Selection of foraging sites varies with temporal changes in goose density during the day
Time × Food resources	Selection for the highest nutritional resources weaken as goose density increases (morning and evening)
Central-place foraging (CPF)	
Distance to roost	Geese reduce selection of foraging sites with increasing distance from roosts
Distance to roost × Food resources	Geese increase selection for the highest nutritional food resources as the distance from roost sites increases while showing no distinct selection for food resources close to roost sites
Predation/disturbance risk (PD)	
Field area	Geese select strongest for foraging sites in larger fields
Field area × Food resources	Geese select strongest for foraging sites in larger fields that contain the highest nutritional value
DD and CPF	
Time × Distance to roost	Geese reduce selection of foraging sites at increasing distance from roost sites when the density of geese around the roosts is low (middays) and increase selection of foraging sites at increasing distance from roost sites when the density around the roosts is high (morning and afternoon)
DD and PD	
Time × Field area	Geese increase selection of foraging sites in larger fields when the density of geese is low (middays) and decrease selection of foraging sites in larger fields when the density is high (morning and afternoon)
PD and CPF	
Field area × Distance to roost	Geese increase selection of foraging sites in larger fields at increasing distance from roost sites

their migration to the breeding grounds, the geese stop in Trøndelag in mid-Norway, and Vesterålen in north-Norway (Madsen et al. 1999). Mid-Norway is semi-mountainous and characterized by a patchwork of agricultural fields and forests. The area is rich in lakes and coastal areas, both of which serve as roost sites for the geese (Fig. 1). Geese are rarely seen resting on the fields and therefore the above-mentioned roosting sites constitute their main resting places. Roosting sites are also the main sources of drinking water for geese and usually located in the remote places, further away from settlements and roads. The location of roosts sites is mapped every year by trained observers and appears constant over

time. Geese use roost sites mainly at night but also parts of the day, particularly around middays (Madsen et al. 1997). 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) (Fig. 2A).

There are four main food resources available to geese in this area: grass, barley stubble from the preceding autumn, newly sown/germinating barley grains, and ploughed barley stubble. These four food resources are henceforth referred to as grass, stubble, grain and ploughed. The geese occasionally

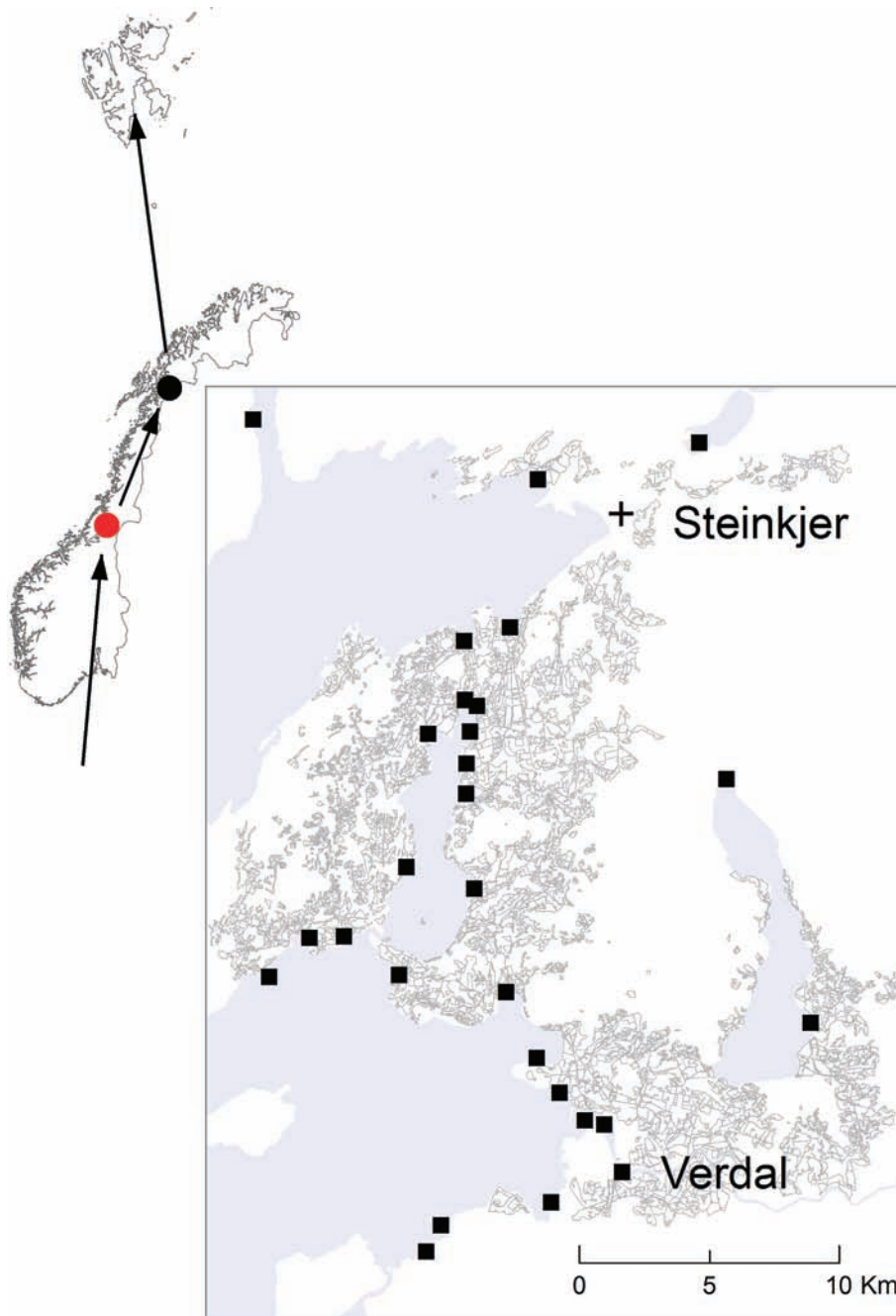


Figure 1. Map of the study area (28 × 33 km) in nord-Trøndelag, mid-Norway, showing all the recorded agricultural fields (grey polygons) within 5 km from roost sites (black squares). Water is marked with light blue. The map in the upper left corner shows the spring migration route of pink-footed geese with the mid-Norway study area marked in red and north-Norway stopover site in black.

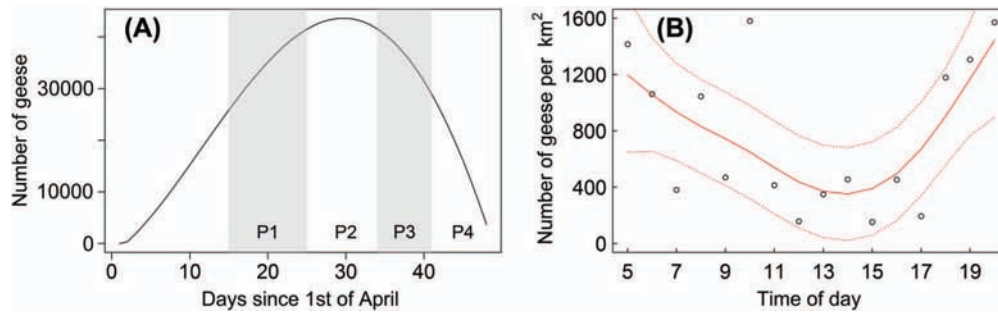


Figure 2. (A) Changes in number of pink-footed geese during spring stopover season in mid-Norway. Due to changes in food resource availability, the stopover season was divided into four periods (P1–P4) in order to study within seasonal changes in habitat selection of geese. (B) Average diurnal changes in density of geese (km^2) observed foraging on fields. The solid red line shows the fitted values from a generalized additive model (GAM: $F_{1,16} = 3.53$, $p = 0.03$) using a non-parametric smoother function and the dotted red lines represent the 95% confidence interval.

forage on waste potato fields but this food resource is very scarce in the study area. Time-activity budgets for pink-footed geese in mid-Norway revealed that ploughed fields are mainly used as resting sites (M. Chudzinska and B. A. Nolet unpubl.). Grass starts growing at the end of April and is readily available during the entire stopover season (Bjerke et al. 2014). Stubble fields are gradually ploughed and subsequently sown with barley, which starts germinating towards the end of the stopover season in mid-May (Madsen et al. 1997). Stubble is the most energetic food resource of all widely available food resources and is 2.8 times more energetic than grain and grass, which are comparable in energetics (Chudzinska et al. unpubl.). Grass, however, is the most protein-rich food resource out of all available at the study site (Prop and Spaans 2004).

In mid-Norway geese are occasionally hunted by white-tailed eagles *Haliaeetus albicilla* (Madsen et al. 1998), but human disturbance (which can also be regarded as predation risk; Tombre et al. 2005, Klaassen et al. 2006) is more frequent at the study site and is believed to be the main risk factor perceived by geese (Madsen 1998).

Sampling of goose presence and food resource availability

Because the availability of food resources in our study site changes dynamically from year to year and within the season we could not rely on standard land cover maps of mid-Norway as they would likely be incorrect at the resolution necessary here. Map errors can seriously bias estimates of habitat selection (Johnson and Gillingham 2008) and we therefore mapped the availability of the different food resources manually within a 28×33 km area between Steinkjer, Verdalen and Inderøy municipalities, which we believe is representative for the mid-Norway stopover site. Arable land (crops and pastures) constituted 12% of the study area and was the only habitat type where geese were observed foraging. Mountain areas/forests (55%) and water (mainly fjords and lakes; 31%) were dominant habitat types at the study site. Settlements and roads made up 2% of the study area. In order to map the study area, we selected all agricultural fields < 5 km from the roost sites, which is the area where most geese forage (Jensen et al. 2008) and all parts were accessible to geese (Fig. 1). For these fields we applied a stratified ran-

dom design to determine the availability of food resources at different distances from roost sites and to determine how the use of the fields changed during the stopover season. The season was divided into four periods of approximately 8 days based on the frequency of food resources mapping surveys. The periods roughly corresponded to habitat changes due to agricultural practices. Period 1 lasted from 15–25 April, period 2 from 26 April–3 May, period 3 from 4–11 May and period 4 from 12–19 May. We randomly selected 900 fields out of 2900 available for each period, which were equally distributed between distances to the roost sites (0–1; 1–2; 2–5 km) and within the study site. In order to get an equal spatial representation of the study area, the survey area was sub-divided into 28 squares of 5×5 km which contained all the selected fields (squares which only contained water were excluded). Each square was visited once per period. During each period the squares were visited in a random order, and all the randomly selected fields and those directly bordering these were surveyed. Each visited field was classified as grass, stubble, grain or ploughed and it was noted if geese were present at the time. Flock size was counted to nearest 10 individuals. The mapping effort was equally distributed between 05:00–21:00 hours. For further analysis we merged all neighbouring fields with the same food resource that were not separated by any physical object (road, forest etc.). Merging of the fields, calculation of distances to the closest roost sites and field area were performed in ArcGIS ver. 10.1 (ESRI 2010 <www.esri.com>). The average field size after merging was 0.3 km^2 .

Resource selection functions (RSFs)

We estimated habitat selection of geese by modelling resource selection functions (RSFs), defined as any function that is proportional to the probability of use by an organism (Manly et al. 1993). RSFs compare environmental conditions at animal locations (e.g. food resource, density, distance to roost) to the attributes at random (i.e. available) points (Boyce and McDonald 1999, Manly et al. 2002). In our RSFs the used points were all the fields where goose presence was observed during the survey and available points were all the remaining surveyed fields (randomly selected fields and all the fields directly bordering the random fields) (Table 2). Although such a sampling design resembles that of used vs

Table 2. The number of ‘used’ and ‘available’ sites surveyed during the four defined periods within the spring stopover season of pink-footed geese in mid-Norway. ‘Sum(unique)’ refers to a number of unique fields visited over the four periods.

	Period 1	Period 2	Period 3	Period 4	Sum(unique)
Use	36	60	80	69	189
Availability	912	1260	1079	1175	2184

unused data, which may be modelled using a resource selection probability function (RSPFs), we could not be certain that the unused sites in our dataset remained so during other times of the day or season outside our field visits. As such, we considered these fields ‘available’ rather than ‘unused’ and continued our analyses with RSFs rather than RSPFs. Moreover, by separating all used sites from the availability sample we removed any potential contamination of the data (i.e. when available sites are in fact used), which leads to robust RSFs and facilitates model inference (Johnson et al. 2006). Our RSF analyses corresponded most closely to that of the landscape-scale, equivalent to the second-order selection of Johnson (1980), and were based on population-level use–availability sampling designs (Design I; Thomas and Taylor 2006). RSFs were computed using generalised linear models (GLMs) for binomial data, performed in R 3.0.1 (<www.r-project.org/>).

Because availability of the different food resources changed over the stopover season, we constructed separate RSFs for each period to exclude potential bias of functional responses in habitat selection (Mysterud and Ims 1998). For each period, we considered ten different RSFs, which were constructed a priori and specifically followed predictions of habitat selection theory (maximising nutrient intake, central-place foraging, predation and density frameworks and a combination of these frameworks as explained in the Introduction and Table 1). Our maximising nutrient intake RSF model included only food resources (four-class categorical variable: grain, grass, ploughed and stubble, with stubble being a reference category because this is the most energetic food resource) as the only independent variable. The number of food resources considered in the RSFs differed between periods, as grain was not present during period 1. Our density-dependent (DD) habitat selection RSFs included time of day (both linear and squared) as the only explanatory variable because the majority of geese forage in the mornings and evenings and spent time on a roost site around midday (Madsen et al. 1997, Chudzińska et al. 2013). This allowed us to use time of day as a proxy for goose density as the number of geese foraging on fields will vary during a day with highest density in the mornings and evenings and lowest around midday (Fig. 2B). Using time of day as proxy for density instead of using goose density/abundance directly in the RSF allowed us to determine whether goose behaviour differs during periods when density is decreasing (morning – when competition declines) or increasing (evening – when competition rises) (Fig. 2B). Using goose density/abundance directly might mask such behavioural differences over time when density/abundance is equal (e.g. at 9:00 am and 17:00 pm; Fig. 2B). We let time of day interact with food resources as an additional density-dependent RSF model. Our central-place foraging (CPF) model used distance to roost site as

explanatory variable, in addition to the interactions with food resources in a second CPF model. Our predation and disturbance (PD) RSF model was constructed using field area size as the major explanatory variable, as we assumed that larger fields are less disturbed and make it easier for geese to detect potential predators. We also let field area interact with food resources as an additional predation/disturbance risk RSF model. Finally, we fitted three RSFs models using combinations of the different habitat selection frameworks. As such, our DD and CPF RSF model included an interaction between time of day and distance to roost. Our DD and PD model included an interaction between time of day and field area and finally our PD and CPF model included the interaction between field area and distance to roost (Table 1).

The outcome of our RSFs (logistic regression using GLM) are a population level estimate of the log-odds ratio of using a site or given resource in the study area. Because we employed used vs available sampling design we could not derive absolute probabilities of use (as in RSPFs) and we calculated the odds ratio of selection (relative probability of use) instead. By taking the log of the odds ratio the outcome becomes more intuitive, as any value below 0 indicates that a given site or resource unit is used less than available, while any value above 0 reflects that a given resource unit is used more than available. Values overlapping with 0 indicate that use of a given resource unit is proportional to availability (i.e. no selection). Indeed, calculation of log-odds ratios of a resource unit (a continuous variable) or relative to a reference level (for a categorical variable) is informative and common in RSF analyses (Godvik et al. 2009, Blix et al. 2014).

In order to successfully manage species and their environment, a prerequisite is to accurately predict their habitat selection patterns (Boyce and McDonald 1999). As such, and to determine which RSF model best predicted habitat selection patterns, we employed the k -fold cross-validation procedure as proposed by Fielding and Bell (1997) and Boyce et al. (2002). This procedure withholds a fraction of the data using a k -fold partitioning, where k represents the number of partitions (so called test-training sets) (Fielding and Bell 1997). To examine model performance, the pattern of predicted RSF scores for partitioned test-training sets is investigated against categories of RSF scores (bins) (Boyce et al. 2002). For the k -fold cross-validation procedure, we calculated Spearman rank correlations (r_s) between ten RSF-bin ranks and five test-training sets ($k = 5$). We repeated this procedure 100 times to determine whether the r_s were significantly different from random (t-test). To identify which models best predicted habitat selection, we considered for each period the two models with the highest r_s value. We chose the k -fold cross-validation procedure over a model selection procedure based on AIC (Akaike 1987), as AIC values are a tradeoff between the goodness of fit and the complexity of the model rather than a degree of prediction accuracy.

Results

Grain, grass, stubble and ploughed were dominant food resources of geese within the study area (Fig. 3A). Fields with waste potatoes constituted only 0.2% of the area

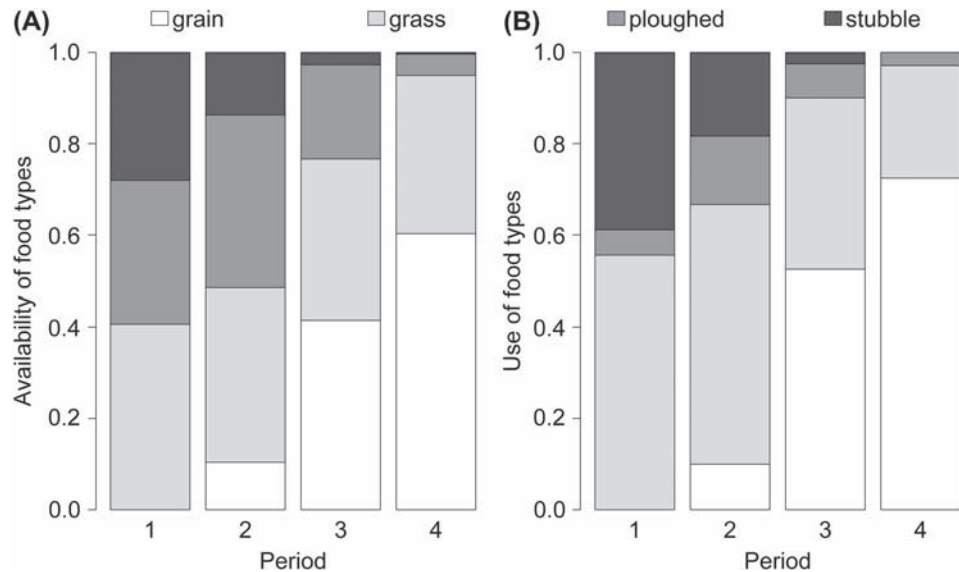


Figure 3. Proportion of four dominant food resources available (A) and used (B) by pink-footed geese at the spring migration stopover site in mid-Norway.

covered by the studied agricultural fields. The availability of grass fields did not change during the study period and consisted on average 36% of all available food resources. The proportion of stubble decreased over the season and was almost absent in period 3 and 4. The availability of ploughed fields also decreased when the season progressed. Grain was absent in the first period; then its availability increased, to become dominant in period 3 and 4 (Fig. 3A). Our survey data suggested that, for each period, use of the different main foraging food resources (grain, grass and stubble) by geese did not differ from availability and that ploughed fields were the only food resource that was used less than expected based on its availability (log-likelihood χ^2 -statistics (Manly et al. 2002): period 1: $\chi_L^2 = 0.01$, $p = 0.99$, period 2: $\chi_L^2 = 1.09$, $p = 0.58$, period 3: $\chi_L^2 = 0.64$, $p = 0.73$, period 4: $\chi_L^2 = 4.32$, $p = 0.12$) (Fig. 3A–B). This indicates that food resources alone did not determine habitat selection of geese. This is corroborated by the fairly low k -fold cross validation values for the maximizing nutrient intake RSF models (Table 3).

The k -fold cross validation score of all RSFs (r_s and p -values of Spearman rank correlations) was significantly higher than expected from random, though we observed substantial variation in predictive performance among models. The predation/disturbance model (PD) including only field area was the model with the highest predictive capacity for period 2 to 4 (mean $r_s = 0.78$, $p < 0.001$, Table 3). Overall, larger fields were used more than available and this tendency did not change between period 2–4, although geese selected larger fields in period 4 than in the previous periods (Fig. 4). The density-dependent RSF model (DD) and the central-place foraging model (CPF) did not predict habitat selection very well independently, but the combination of these models was the best predictor for period 1 and did rank among the two top models during period 2–3 (mean $r_s = 0.73$, $p < 0.001$, Table 3). During the first period, the relative probability of observing geese was highest close to the roost site, as expected by CPF framework ($\log[\text{odds}$

$\text{ratio}]_{\text{close to roost}} > \log[\text{odds ratio}]_{\text{away from roost}}$, Fig. 5A). Furthermore, the relative probability of observing geese declined as distance from roost sites increased, a pattern that was evident for all times of the day. During period 2 and 3 when densities of geese at the stopover site were highest, geese used areas close to the roost sites proportional to availability regardless of time of day ($\log[\text{odds ratio}]$ is close to 0 at distance close to roost sites for all time of day; Fig. 5B–C). During the same periods, the relative probability of using areas further from the roost sites declined in the mornings ($\log[\text{odds ratio}] < 0$ at distances further away from roost sites) but increased in the evenings ($\log[\text{odds ratio}] > 0$ as distance from roost sites increased; Fig. 5 B–C).

Discussion

All theory-based habitat selection models considered here were able to predict the spatiotemporal distribution of migratory pink-footed geese at their spring stopover site in mid-Norway. However, predictive performance varied substantially between models and temporal scales (both within stopover season as well as on a diurnal basis). We found most support for the predation/disturbance risk model and for the combined density-dependent and central-place foraging models.

Capital breeders, such as pink-footed geese, are expected to maximise nutrient (fat and protein) intake along the migration route in preparation of the upcoming breeding period. Nevertheless, our habitat selection model based purely on maximising nutrient intake rules did not appear among the top-ranked models. This suggests that the nutritional value of the available food resources is not a major limiting factor of the habitat selection patterns of geese in this area. We found that geese used most food resources proportional to their availability, indicating that foraging sites were chosen independently of food quality. This finding is likely influenced by the overall high quality of the food resources

Table 3. Overview of the k -fold cross-validation procedure showing the Spearman-rank correlations (r_s) for all RSF models. For each period, the models that best and second best predicted habitat selection of pink-footed geese at their mid-Norway stopover site are shown in bold and italics respectively. k -fold cross-validation values were calculated using 10 RSF bins and 5 test-training sets. This procedure was repeated 100 times. n.par shows number of parameters in the RSF model. Note that the number of parameters used in the same model differed between periods as the number of available food resources varied between periods. All r_s -values were statistically different from random at $p < 0.05$ unless indicated by a superscript.

	Period 1		Period 2		Period 3		Period 4	
	n.par	r_s	n.par	r_s	n.par	r_s	n.par	r_s
Maximising nutrient intake								
Food resources	3	0.61*	4	0.55	4	0.60*, ¹	4	0.41
Density-dependent habitat selection (DD)								
Time	3	0.47	3	0.42	3	0.67	3	0.21
Time × Food resources	9	0.50	12	0.42	12	0.63	12	0.60
Central-place foraging (CPF)								
Distance to roost	2	0.52	2	0.56	2	0.61	2	0.55
Distance to roost × Food resources	6	0.52	8	0.63	8	0.58	8	0.65
Predation/disturbance risk (PD)								
Field area	2	0.63	2	0.74	2	0.80	2	0.81
Field area × Food resources	6	0.54	8	0.65	8	0.71	8	0.73
DD and CPF								
Time × Distance to roost	6	0.68	6	0.73	6	0.77	6	0.59
DD and PD								
Time × Field area	6	0.55	6	0.69	6	0.70	6	0.69
PD and CPF								
Field area × Distance to roost	4	0.59	4	0.48	4	0.65	4	0.70

* k -fold value were calculated using 5 bins and 50 test-training sets as models did not converge using the settings employed in the other RSFs.

¹ $p = 0.02$

available in the landscape as stubble and grain are a good source of energy and grass is rich in protein. As such, choosing one forage resource over the other might not provide much benefit in terms of nutrient gain. Furthermore, the geese are foraging in a highly dynamic, agricultural landscape where the food type on a given patch may change from one day to the next. In such a scenario, where individuals are unlikely to have sufficient knowledge about the environment, choosing patches at random may be more

beneficial than returning to a previously visited patch as it reduces searching time and energy expenditure (Amano et al. 2006a, b). Similar random choice of foraging habitat has been found for other species living in highly dynamic landscapes (e.g. fallow deer *Dama dama*: Focardi et al. 1996). The only fields that geese used less than proportional were barren ploughed. This is, however, to be expected, as there is no energetic benefit from spending time on this food resource.

The predation/disturbance risk model including field size as the main explanatory variable best predicted habitat selection of geese for almost the complete stopover season. This finding corroborates previous results that the behaviour of pink-footed geese along the complete migration route is strongly influenced by disturbances (Madsen 1994, 1998, Chudzińska et al. 2013, Simonsen 2014). Indeed, disturbance and related predator avoidance behaviour is known to be an important factors shaping habitat selection of variety of species across different taxa (Blaustein et al. 2004, Pierce et al. 2004, Creel et al. 2005). There are many sources of disturbances in our study area (e.g. passing cars, small planes, intentional scaring) and disturbance levels are typically lower on large fields compared to smaller fields (Amano et al. 2006a). Moreover, foraging on large open fields is considered an effective antipredator strategy in many species (e.g. white-fronted geese *Anser albifrons*, Amano et al. 2006a; mule deer *Odocoileus hemionus*, Altendorf et al. 2001).

The Svalbard-breeding population of pink-footed geese has increased from approximately 15 000 individuals in the 1960s to around 80 000 in 2012 (Madsen and Williams 2012), however no density dependent effect has been observed so far during overwintering, migration

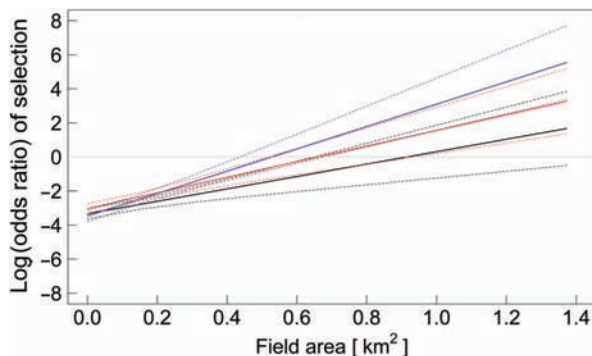


Figure 4. Estimates of selection for field area during periods 2–4 (log odds ratio \pm 95% confidence intervals) by pink-footed geese at the mid-Norway stopover site as computed by the predation/disturbance risk RSF model with field area as the only predictor variable. Black line: period 2; red line: period 3; blue line: period 4. Estimates overlapping 0 (grey, horizontal line) indicate that the use is proportional to the availability ('no selection'), estimates higher than 0 indicate use higher than availability whereas values below 0 indicate use below availability for a given site.

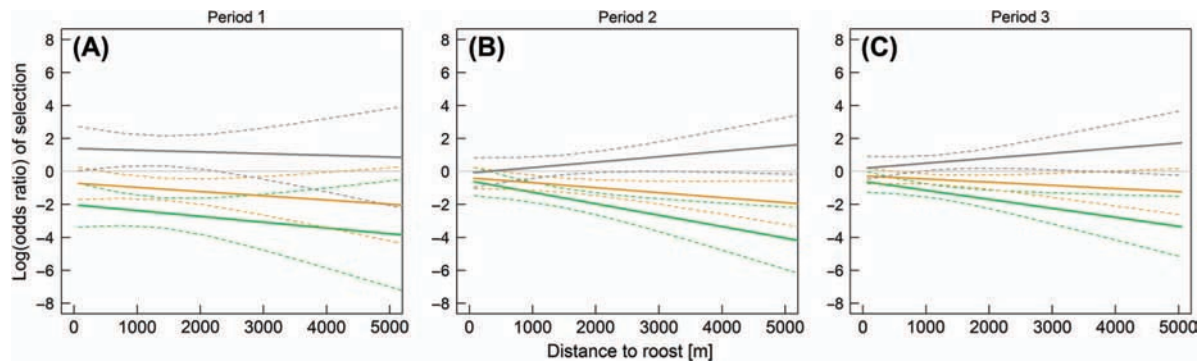


Figure 5. Estimates of selection for sites at increasing distance from roost sites at different times of the day (log odds ratio \pm 95% confidence intervals) by pink-footed geese at the mid-Norway stopover site as computed by the density-dependent/central-place foraging RSF model with time of day (green line: morning (05:00–11:00); brown line: midday (11:00–16:00); grey line: evening (16:00–21:00)) and distance to the closest roost site as the predictor variables. Estimates overlapping 0 (grey, horizontal line) indicate that the use is proportional to the availability ('no selection'), estimates higher than 0 indicate use higher than availability whereas values below 0 indicate use below availability for a given site.

or breeding season (Kéry et al. 2006, Jensen et al. 2014). Although the predictive performance of the central-place foraging and the density-dependent RSF models did not rank among the highest, the combination of these models revealed that variation in both local density and distance from the focal point (roost site) do influence habitat selection of geese both over the stopover season and during a day. In the mornings, when all geese leave roost sites to forage, geese behaved like 'classical' central-place foragers, with a higher relative probability to stay close to the roost. At middays, when densities on fields were lowest, 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. If many birds are searching for suitable foraging patches around the same focal area, birds that depart from roost sites later in a day may be unable to find an unoccupied patch close to this area and are subsequently forced to select areas further away. We suggest that the cumulative effect of increasing densities and intraspecific competition over the day may force birds to search for available foraging sites further away from roost sites in the evening. The predictive capacity of the combined central-place foraging and density-dependent models was high only during the periods when the population was growing and therefore intraspecific competition was relatively low (period 1 when not all geese have arrived at the stopover site, Madsen et al. 1999) or at its peak (period 2 and 3). At the end of the stopover season (period 4) when density is declining rapidly because geese depart the area, the combined model predicted habitat selection of geese substantially less well (Fig. 2A).

Contrary to predictions of the central-place foraging theory, we did not find strong support for the model predicting an increase in selection of high-quality food types with increasing distance from the focal point (distance to roost \times food resources model). This theoretical prediction is made under the assumptions that food quality is heterogeneously distributed and high-quality food resources are rapidly depleted close to the central-place due to increased competition (Rosenberg and McKelvey 1999). However, forage depletion is unlikely to be a factor in our study as

the stopover site is used at the onset of the growing season leading to the increased availability and quick turnover of high-quality food resources. Indeed, a resource depletion model developed for our study site and based on the same field selection (all fields $<$ 5 km from roost sites) showed that the amount of food resources available is sufficient to accommodate the current number of geese (Baveco et al. pers. com.). What defines the central-place foraging pattern is therefore not directly the quality or availability of food resources but the changes in goose density and intraspecific competition for unoccupied patches.

Arable landscapes offer a readily accessible and highly nutritional food source which has led to an apparent increase in the use of pastures and agricultural crops by a variety of species (e.g. roe deer *Capreolus capreolus*: Cibien et al. 1989, various goose species: Madsen et al. 1999, Fox et al. 2005, buff-breasted sandpipers *Tryngites subruficollis*: McCarty et al. 2009). However, foraging in agricultural landscapes results in higher exposure to human presence compared to more natural and remote areas which can greatly influence habitat selection of birds (such as geese as in this study), but also of mammals (e.g. roe deer: Hewison et al. 2001). In order to alleviate conflicts between pink-footed geese foraging on arable fields and farming interests, Norwegian authorities have tried to alleviate the conflict by offering an annual fixed area rate payment to land-owners in exchange for providing accommodation areas where geese can forage undisturbed (Madsen et al. 2014). The criteria of such refuges is based on a range of environmental factors including distance to roost sites (Jensen et al. 2008, Madsen et al. 2014, Simonsen 2014). Based on the results from this study and previous observations, field size and goose density are important additional factors on which the location of accommodation areas is already based (Madsen et al. 2014).

Comparing among a range of theory-driven habitat selection models, we have shown that in landscapes where nutritional value of food resources is homogeneously high, the spatiotemporal distribution and foraging behaviour of pink-footed geese is largely a tradeoff between fast refuelling and disturbance/predator avoidance. The analytical framework we adopted here can serve as a basis to try and understand

habitat selection patterns of other species as most factors considered here are known to influence the behaviour of most free-ranging animals (birds as well as mammals). Especially the foraging behaviour of species that regularly return to a central-place and forage in large groups in landscapes with anthropogenic disturbances may be influenced by a combination of environmental factors in a similar manner to those observed for pink-footed geese in our study. Overall, one single framework may be insufficient to explain the observed variation in foraging behaviour of animals as multiple conditions are expected to influence habitat selection patterns.

Acknowledgements – This study was part of MC's PhD project funded by Aarhus University. The fieldwork was supported by the Norwegian Research Council project MIGRAPOP. We would like to thank Jannik Hansen and Robert Peel for help during data collection.

References

- Akaike, H. 1987. Factor analysis and AIC. – *Psychometrika* 52: 317–332.
- Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy, and safety. – In: Gwinner, E. (ed.), *Bird migration*. Springer, pp. 331–351.
- Altendorf, K. B. et al. 2001. Assessing effects of predation risk on foraging behavior of mule deer. – *J. Mammal.* 82: 430–439.
- Amano, T. et al. 2006a. Foraging patch selection and departure by non-omniscent foragers: a field example in white-fronted geese. – *Ethology* 112: 544–553.
- Amano, T. et al. 2006b. Decision-making in group foragers with incomplete information: test of individual-based model in geese. – *Ecol. Monogr.* 76: 601–616.
- Bauer, S. et al. 2008. The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic geese. – *J. Anim. Ecol.* 77: 654–660.
- Bjerke, J. W. et al. 2014. Reduced dairy grassland yields in central Norway after a single springtime grazing event by pink-footed geese. – *Grass Forage Sci.* 69: 129–139.
- Blaustein, L. et al. 2004. Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. – *Oecologia* 138: 300–305.
- Blix, A. W. et al. 2014. Temporal scales of density-dependent habitat selection in a large grazing herbivore. – *Oikos* 123: 933–942.
- Boyce, M. S. and McDonald, L. L. 1999. Relating populations to habitats using resource selection functions. – *Trends Ecol. Evol.* 14: 268–272.
- Boyce, M. S. et al. 2002. Evaluating resource selection functions. – *Ecol. Modell.* 157: 281–300.
- Chudzińska, M. et al. 2013. Diurnal variation in the behaviour of the pink-footed goose (*Anser brachyrhynchus*) during the spring stopover in Trøndelag, Norway. – *J. Ornithol.* 154: 645–654.
- Cibien, C. et al. 1989. Influence of habitat characteristics on winter social organization in field roe deer. – *Acta Theriol.* 34: 219–226.
- Creel, S. et al. 2005. Elk alter habitat selection as an antipredator response to wolves. – *Ecology* 86: 3387–3397.
- Drent, R. et al. 1978. Balancing the energy budget of arctic-breeding geese throughout the annual cycle; a progress report. – *Verh. Ornithol. Gesellschaft Bayern* 23: 239–264.
- Drent, R. H. et al. 2003. Pay-offs and penalties of competing migratory schedules. – *Oikos* 103: 274–292.
- Fielding, A. H. and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. – *Environ. Conserv.* 24: 38–49.
- Focardi, S. et al. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. – *J. Anim. Ecol.* 65: 606–620.
- Fox, A. D. et al. 2005. Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. – *Global Change Biol.* 11: 881–893.
- Godvik, I. M. R. et al. 2009. Temporal scales, tradeoffs and functional responses in red deer habitat selection. – *Ecology* 90: 699–710.
- Hedenström, A. and Alerstam, T. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. – *J. Theor. Biol.* 189: 227–234.
- Hewison, A. J. et al. 2001. The effects of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. – *Can. J. Zool.* 79: 679–689.
- Jensen, R. et al. 2008. Prioritizing refuge sites for migratory geese to alleviate conflicts with agriculture. – *Biol. Conserv.* 141: 1806–1818.
- Jensen, G. H. et al. 2014. Snow condition as an estimator of the breeding output in high-Arctic pink-footed geese *Anser brachyrhynchus*. – *Polar Biol.* 37: 1–14.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. – *Ecology* 61: 65–71.
- Johnson, C. J. and Gillingham, M. P. 2008. Sensitivity of species-distribution models to error, bias, and model design: an application to resource selection functions for woodland caribou. – *Ecol. Modell.* 213: 143–155.
- Johnson, C. J. et al. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. – *J. Wildl. Manage.* 70: 347–357.
- Jonker, R. M. et al. 2010. Predation danger can explain changes in timing of migration: the case of the barnacle goose. – *PLoS ONE* 5: e11369.
- Kéry, M. et al. 2006. Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. – *J. Anim. Ecol.* 75: 1172–1181.
- Klaassen, M. et al. 2006. Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. – *J. Appl. Ecol.* 49: 92–100.
- Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – *Can. J. Zool.* 68: 619–640.
- Lindström, Å. 1990. The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. – *Behav. Ecol.* 1: 102–106.
- Lindström, Å. 1991. Maximum fat deposition rates in migrating birds. – *Ornis Scand.* 22: 12–19.
- Madsen, J. 1994. Impacts on disturbance on migratory waterfowl. – *Ibis* 137: S67–S74.
- Madsen, J. 1998. Changing tradeoffs between predation risk and food intake: gaining access to feeding patches during spring-fattening in pink-footed geese *Anser brachyrhynchus*. – *Norw. Polarinst. Skrifter* 200: 305–312.
- Madsen, J. and Williams, J. H. 2012. International species management plan for Svalbard population of the pink-footed goose *Anser brachyrhynchus*. – *AEWA Tech. ser.* 48.
- Madsen, J. et al. 1997. Spring migration strategies and stopover ecology of pink-footed geese. Results of field work in Norway, 1996 (Laursen, K. ed.). – *NERI Tech. Rep.* No. 204
- Madsen, J. et al. 1998. Correlates of predator abundance with snow and ice conditions and their role in determining timing of nesting and breeding success in Svalbard light-bellied brent

- geese *Branta bernicla hrota*. – Norw. Polarinst. Skrifter 200: 221–234.
- Madsen, J. et al. 1999. Pink-footed goose *Anser brachyrhynchus*: Svalbard. – In: Madsen, J. et al. (eds), Goose population of the Western Palearctic. Wetlands Int. Publ. No. 48, Natl Environ. Res. Inst., Denmark, pp. 82.
- Madsen, J. et al. 2014. Regional management of farmland feeding geese using an ecological prioritization tool. – *Ambio* 43: 801–809.
- Manly, B. F. J. et al. 1993. Resource selection by animals: statistical design and analysis for field studies. – Chapman and Hall.
- Manly, B. J. F. et al. 2002. Resource selection by animals: statistical design and analysis of field studies. – Kluwer.
- McCarty, J. P. et al. 2009. Behavior of buff-breasted sandpipers (*Tryngites subruficollis*) during migratory stopover in agricultural fields. – PLoS ONE 4: e8000.
- McDonald, P. et al. 1973. Animal nutrition. – Oliver and Boyd.
- McLoughlin, P. D. et al. 2010. Considering ecological dynamics in resource selection functions. – *J. Anim. Ecol.* 79: 4–12.
- Mysterud, A. and Ims, R. A. 1998. Functional responses in habitat use: availability influences relative use in tradeoff situations. – *Ecology* 79: 1435–1441.
- Orians, G. H. and Pearson, N. E. 1979. On the theory of central place foraging. – Ohio State Univ. Press, Columbus, OH.
- Pierce, B. M. et al. 2004. Habitat selection by mule deer: forage benefits or risk of predation? – *J. Wildl. Manage.* 68: 533–541.
- Prop, J. and Black, J. M. 1998. Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats. – Norw. Polarinst. Skrifter 200: 175–193.
- Prop, J. and Spaans, B. 2004. Body stores in pre-migratory brent geese: the consequence of habitat choice on protein deposition. – In: Food finding. On the trail to successful reproduction in migratory geese. PhD thesis, pp. 71–85.
- Robbins, C. T. 1993. Wildlife feeding and nutrition. – Academic Press.
- Rosenberg, D. K. and McKelvey, K. S. 1999. Estimation of habitat selection for central-place foraging animals. – *J. Wildl. Manage.* 63: 1028–1038.
- Rosenzweig, M. L. 1981. A theory of habitat selection. – *Ecology* 62: 327–335.
- Schoener, T. W. 1979. Generality of the size–distance relation in models of optimal feeding. – *Am. Nat.* 114: 902–914.
- Shochat, E. et al. 2002. Density-dependent habitat selection in migratory passerines during stopover: what causes the deviation from IFD? – *Evol. Ecol.* 16: 469–488.
- Sih, A. 1980. Can foragers balance two conflicting demands? – *Science* 210: 1041–1043.
- Simonsen, C. E. 2014. Goose/agricultural conflicts in Norway – building species distribution models: objective tools in local management when allocating subsidies and evaluations on scaring cost effectiveness. – Aarhus Univ. <www.gint.no>.
- Stephens, P. A. et al. 2014. Capital and income breeding: the role of food supply. – *Ecology* 95: 882–896.
- Sunde, P. and Redpath, M. 2006. Combining information from range use and habitat selection: sex-specific spatial responses to habitat fragmentation in tawny owls *Strix aluco*. – *Ecography* 29: 152–158.
- Thomas, D. L. and Taylor, E. J. 2006. Study designs and tests for comparing resource use and availability II. – *J. Wildl. Manage.* 70: 324–336.
- Tombre, I. et al. 2005. Influence of organised scaring on distribution and habitat choice of geese on pastures in northern Norway. – *Agric. Ecosyst. Environ.* 111: 311–320.
- van Beest, F. M. et al. 2014. Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal. – *J. Anim. Ecol.* 83: 147–156.
- van Gils, J. A. and Tijssen, W. 2007. Short-term foraging costs and long-term fueling rates in central-place foraging swans revealed by giving-up exploitation times. – *Am. Nat.* 169: 609–620.
- Weber, T. P. et al. 1998. Optimal avian migration: a dynamic model of fuel stores and site use. – *Evol. Ecol.* 12: 377–401.