

Matching a Changing World -
the Importance of Habitat
Characteristics for Farmland Breeding
Eurasian Curlew

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Cover: Pair of Eurasian curlews deciding where to put their nest.
(photo: Kjell Sjöberg)

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Abstract

Where animals are and what they do, is the result of a continuous cost-benefit analysis of available alternatives. Choices have to be made, for example when settling in a breeding territory after migration, when foraging conditions change, when humans change the landscape, or when a predator approaches the nest. In this thesis, I used Eurasian curlew data to address these issues at the national, landscape and agricultural field level.

The results show that farmland was the most important habitat for the species (appr. four times as important as mires), but that < 40 ha patches of farmland embedded in forest landscapes were seldom used. During the first part of the breeding season, the birds preferred to forage on leys, but later they shifted to cereal fields. No effect of the construction of the Bothnia Line railway on Eurasian curlew densities could be shown. Finally, experimental approaches of nests showed that the chances for hatching success were best when the incubating bird leaved the nest neither very soon nor very late.

Albeit flexible in behaviour, Eurasian curlews seem to demand landscapes that contain sufficiently large patches of farmland, preferably with mixtures of fields under different management.

Keywords: farmland bird, habitat association model, patch size, patch occupancy, foraging habitat, infrastructure, flight initiation distance, wader, agriculture, biodiversity conservation

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Dedication

To Marian, Robin, Laura Linn and Jordi

No man ever steps in the same river twice.

Heraclitus

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List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Adriaan de Jong & Åke Lindström. The relationship between habitat and abundance in Eurasian curlew and northern lapwing over a large latitudinal gradient. (Manuscript)
- II Adriaan de Jong & Lars Edenius. Landscape distribution of Eurasian curlew: does habitat patch size matter? (Manuscript)
- III Adriaan de Jong. (2012). Seasonal shift of foraging habitat among farmland breeding Eurasian curlews. *Ornis Norvegica* 35: 23-27.
- IV Adriaan de Jong & Nils Bunnefeld. A before-during-after control-impact study of railway construction and farmland breeding bird densities. (Manuscript)
- V Adriaan de Jong, Carin Magnhagen & Carl-Gustaf Thulin. Do farmland breeding Eurasian curlew optimize flight initiation distance to maximize hatching probability? (Manuscript)

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The contribution of Adriaan de Jong to the papers included in this thesis was as follows:

- I de Jong main responsible for idea, planning, analysis and text. Lindström responsible for data collection and contributed significantly with idea and text.
- II de Jong main responsible for idea, planning, data collection, analysis and text. Edenius contributed with planning and analysis and contributed significantly with text.
- III de Jong responsible for idea, planning, data collection, analysis and text.
- IV de Jong responsible for idea, planning, data collection, analysis and text. Bunnefeld contributed significantly with analysis and text.
- V de Jong main responsible for idea, planning, data collection, analysis and text. Magnhagen contributed significantly with idea and text, and contributed with planning and analyses. Thulin contributed significantly with text, and contributed with planning and analyses.

Abbreviations

AIC	Akaike Information Criterion
AICc	Corrected Akaike Information Criterion
BACI study	Before-After Control-Impact study
BDACI study	Before-During-After Control-Impact study
BMI	Body Mass Index
CI study	Control-Impact study
FID	Flight Initiation Distance
GIS	Geographic Information System
SBS	Swedish Bird Survey

1 Introduction

Outside the world of quantum physics, any material entity is at a certain place at a given time (Mehra & Rechenberg, 1982). The question is why there just then? The distribution of matter in time-space is fascinating in the abiotic world, but even more intriguing in the world of living organisms, due to their limited lifespan, their dependency of adequate environmental conditions, and their interactions with other organisms.

1.1 Choice to move

For mobile life forms, spatio-temporal positioning contains an element of choice. Being an immigrant myself, I've been confronted with the "Why did you move?" question many times (sometimes even by myself!). I doubt that people who did not migrate are asked the "Why did you stay?" question very often. Logically, these two questions are equally relevant. Consequently, the current position of any mobile organism always depends on the outcome of "Should I stay or should I go somewhere else?" decisions. These decisions and the spatial patterns their outcomes create are the topics of this thesis.

The decision to leave its current position or not is made by the individual, and an underlying assumption is that the choice always falls on the best available option. As a result of natural selection (Darwin, 1859), this is a plausible assumption for individuals within a population in general, but given the complexity and the context dependency of real world decisions, this assumption is hard to test for specific choices made by specific individuals.

At the population level, fitness measurements can be used to test possible mismatches between habitat selection and habitat quality (Gilroy *et al.*, 2011). Such a mismatch can lead to an ecological trap situation (Robertson & Hutto, 2006) and cause source-sink patterns at a landscape level (Battin, 2004; Remes, 2000). Pärt *et al.* (2007) propose a two-step model focusing on individual decisions to analyse the presence of ecological traps. These decisions are the

sum of many decisions over a substantial timespan, typically a breeding season.

If mismatches between habitat preference and habitat quality are frequent, the method of counting organisms to measure habitat quality could be misleading (van Horne, 1983). Despite this, the review by Bock and Jones (2004) showed that positive relationships between bird numbers and habitat quality prevail, and for the purpose of the studies in this thesis, it is assumed that birds make well-informed and wise decisions, as individuals as well as collectively. In this context, habitat quality refers to the overall fitness individuals can achieve while living in that particular piece of habitat.

Once the association between habitat and species can be expressed in statistical models, we can use those models to predict the impact of future habitat changes or the occurrences in similar conditions elsewhere (Elith & Leathwick, 2009; Guisan & Thuiller, 2005). The models can also be used to describe historical conditions and developments (e.g. Tingley & Beissinger, 2009). Habitat changes may have natural causes (e.g. floods or fires) or be anthropogenic (e.g. global warming or changed agriculture management). Especially predictions of effects of global warming have received much interest (Bellard *et al.*, 2012; Pearson & Dawson, 2003).

1.2 Changing world

When habitat changes over time, organisms are forced to re-evaluate their former habitat preference decisions, in other words: consider moving. Given the complexity of habitats, some aspects can always be expected to change, regardless the time-frame in focus. For the organism, the challenge lies in staying on top of change, if possible even being ahead of change. At the population or species level this capacity is taken care of by random mutations and adaptive plasticity (Reed *et al.*, 2011; Wolf & Weissing, 2010; Smith & Blumstein, 2008). At the individual level, information retrieval and experience are additional components (Schmidt *et al.*, 2010). At both levels, overall fitness is the ultimate measure of success. As an example of how birds can react to seasonal changes in habitat quality, Gilroy *et al.* (2010) showed that farmland breeding yellow wagtails *Motacilla flava* bred in autumn-sown cereals first, and then moved to potato fields elsewhere in the region for a second breeding attempt. In habitat association models, temporal effects have to be accounted for; a) by thorough evaluation of the underlying datasets, b) through synchronisation of the species and habitat data, and c) by integrating temporal trends in the modelling process.

Ultimately, the place of ovoposition or birth is where the positioning process of an individual starts. Here, the individual inherits the habitat association from its parent(s). Later, the starting point is “Here” (the current position), and the available places to move to are constrained by distance-speed-time-energy equations. Although the non-stop migration of bar-tailed godwits between Alaska and New Zealand (Gill *et al.*, 2006) shows that some animals are amazing dispersers, there will always be limits. Also, the available information decreases with the distance to the possible endpoint of the move, and thus, biases decisions towards nearby endpoints. This makes spatial auto-correlation a necessary component of habitat association models (e.g. Austin, 2002). Social information, including tradition, is a way to extend the information retrieval of the individual, even across taxonomic borders (Seppanen *et al.*, 2007).

Biotic interactions are also part in the location decision-making process. Biotic interactions will often lead to negative density dependency, for example when individuals compete for the same resource or in predator-prey relations. Well known effects of positive interactions are flocking behaviour and colony breeding. Vepsäläinen *et al.* (2007) show the importance of breeding groups for territory occupancy in ortolan bunting *Emberize hortulana*, a less well known form of clustering in bird societies.

Recent technological developments have enabled researchers to follow the movements of free living animals in great detail over long periods of time (e.g. Bunnefeld *et al.*, 2011; Sahlsten *et al.*, 2010), but until the continuous tracking of animals becomes commonplace, most ecological studies will be confined to snapshot descriptions of the distribution of mobile organisms.

1.3 Farmland habitat

Occupying 38% of the world’s land surface, agricultural land is a prevailing component in many landscapes and an important ecosystem. This is where most of our food is produced and where many people make their living and live their lives. Due to the social organisation of many rural societies, the term farmland is commonly used for agricultural land surrounding homes and villages. Arable (tilled) land makes up 28% of the global acreage of agricultural land, in Europe 59% and in Sweden even 86% (<http://faostat.fao.org/>). Tilling adds a high level of disturbance to the ecosystem, and has played an important role in the intensification of agriculture when large areas of natural grasslands, which were previously used as meadows or pastures, were turned into arable land (Antonsson & Jansson, 2011). In the boreal landscape of northern Sweden, arable land is by far the

dominating form of agricultural land use (Statistics Sweden, <http://www.scb.se/>).

1.4 Agriculture and loss of biodiversity

In industrialised countries, the intensification of agriculture (Kleijn *et al.*, 2009), in combination with the abandonment of marginal farmland (Dirk, 2005), has led to substantial loss of biodiversity (Gregory *et al.*, 2004). This causes conservation concern, but also threatens productivity through the loss of ecological services delivered by animals and non-crop plants (Miguel A, 1999). Studies of strategies to solve the agriculture-biodiversity conflict suggest multiple-stakeholder approaches (e.g. Aranzabal *et al.*, 2008; Henle *et al.*, 2008; Mattison & Norris, 2005), and in the meantime, large sums of public money are spent on agri-environment schemes (Whittingham, 2007). The efficiency of these agri-environment schemes has been questioned (Kleijn *et al.*, 2011), but positive effects have been reported (e.g. O'Brien & Wilson, 2011; Davey *et al.*, 2010) and new designs are gradually evolving (e.g. Whittingham, 2011). A current trend is to integrate ecosystem services and conservation (e.g. Rhymer *et al.*, 2010). The future will tell whether these improvements can keep up with economical, technical and political developments in the agricultural sector. In their horizon scan of global conservation issues for 2012 (n=15), Sutherland *et al.* (2012) point at three issues that potentially can have a large impact on agricultural landscapes: (1) sterile farming to increase food safety, (2) transferring nitrogen-fixing ability to cereals, and (3) increased cultivation of perennial cereals. Also mentioned in their list is electrochemical sea water desalination, which could drastically change where and how crops are grown. The development of agricultural practice will surely continue, and so will its influence on farmland biodiversity. Solid knowledge of the organisms and the ecological processes involved will be vital for current and future conservation of farmland biodiversity.

1.5 Farmland bird decline

Farmland birds and their recent decline are extensively studied (e.g. Voříšek *et al.*, 2010). The Common Farmland Bird (CFB) index compiled by the European Bird Census Council (<http://www.ebcc.info/index.php>) has declined by 44% in period 1980-2005. Agricultural intensification is commonly seen as the main cause of farmland bird decline (Anderson *et al.*, 2001). Newton (2004) described intensification as a multi-component process. On arable land, the main components are draining, the use of agro-chemicals, removal of

unproductive landscape elements, crops specialisation and changing management practices (e.g. time of ploughing or harvesting). On pastures, increased livestock densities reduce vegetation structure and increase the risk of trampling. One step in the intensification process may initiate a cascade of successive changes. For example drainage may lead to the use of new crops and more intensive management, which reduces the abundance of non-cropped plants and the invertebrates that depend on them, and finally, influences insect eating birds.

Abandonment of marginal farmland is driven by the same overarching processes as intensification (Dirk, 2005). In the northern parts of Europa, including most of Sweden, abandonment is an important cause of farmland diversity loss. Land that was turned from forest into farmland by settlers hundreds of years ago returns to be forest within decades, and is lost as breeding habitat for, for example, Eurasian skylark *Alauda arvensis*, northern lapwing *Vanellus vanellus* and Eurasian curlew *Numenius arquata*.

1.6 Why Eurasian curlew?

Currently, the agricultural landscapes in the north-eastern parts of Sweden are the stronghold of the Eurasian curlew in Sweden. Here, the species is widely appreciated as “the herald of spring” and functions as a flagship species in farmland biodiversity conservation.

In Europe, the Eurasian curlew is not common enough to be included in the CFB index, but in Sweden the species is included in the index for the environmental target “a rich agricultural landscape” (from Swedish “Ett rikt odlingslandskap”, <http://www.miljomal.se/>). This index started in 2002 and has not shown any significant trend since (Lindström *et al.*, 2012). Contrastingly, the numbers of Eurasian curlew have shown a negative trend: -2.5% year⁻¹ for period 1998-2011, Swedish Bird Survey (Lindström *et al.*, 2012). The Swedish conservation status is Vulnerable (www.artdata.se). Clearly, the Eurasian curlew is of conservation concern.

The Eurasian curlew is an attractive study species because it is a large, long-lived (Fransson *et al.*, 2008), highly mobile, migrating bird that breeds territorially in open, easily accessible landscapes. In addition, their size, display flights and calls make them easy to detect and count. The main disadvantage is that the sexes are not easily separated. Finally, in the eye of the farmer and the local community, a Eurasian curlew researcher earns immediate goodwill, and is allowed almost unlimited access to agricultural fields, private roads and even gardens.

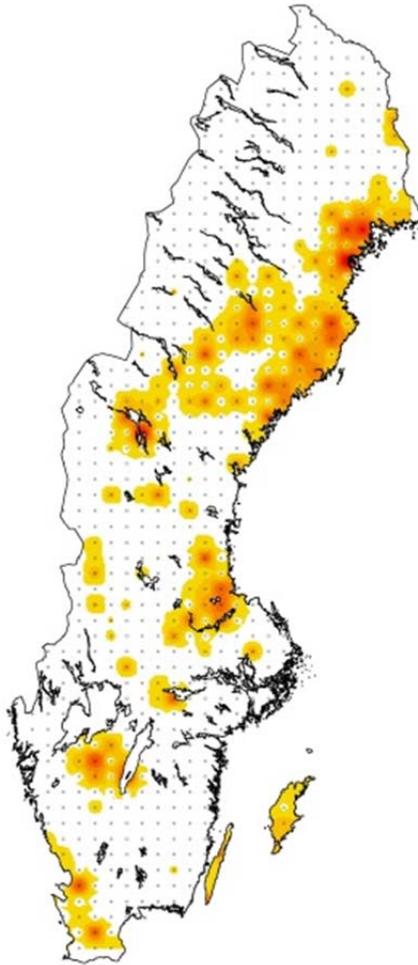


Figure 1. Density distribution map of Eurasian curlew based on distance weight interpolated 2000-2010 SBS route averages. Dots mark the location of the SBS routes, and the white-red colour scale depicts values 0-27 Eurasian curlews per SBS route. The white southern tip of the country is an artefact due to the location of the SBS routes and the external limits of the interpolation method.

2 Objectives

This thesis aims to contribute to the knowledge of the distribution patterns and population trends of farmland birds, with particular focus on the Eurasian curlew; “why they are where they are and where they might be in the future”.

More specifically, the following questions are addressed:

1. What habitat and geographical characteristics do explain the numbers of Eurasian curlew and northern lapwing across Sweden? Paper I
2. Can multiple land cover datasets be combined to produce better species-habitat association models? Paper I
3. What determines whether a farmland patch in a boreal landscape is occupied by Eurasian curlew or not? Paper II
4. Do Eurasian curlews shift between foraging habitats during the breeding season? Paper III
5. Are the populations of farmland breeding birds affected by the construction of a new railway? Paper IV
6. Has incubation behaviour an effect on hatching success in Eurasian curlew? Paper V

3 Materials and methods

In the first two studies, occurrences of Eurasian curlews were correlated to habitat characteristics, and in the next two, we studied the temporal aspects of abundances under the influence of habitat change. The last study is an experimental study of incubation behaviour. With the exception of the first study (Paper I), all studies are based on original data collected during 2002-2010.

In Paper I, we related Swedish Bird Survey Fixed Routes abundances of Eurasian curlew and northern lapwing to habitat variables in the CORINE Land Cover 2000. We developed optimal models for the two species in a mixed effects framework, and discussed the ecological interpretation of the variable composition of the models. We then tested the explanatory power of native and foreign models. Finally we tested if a combination of the two habitat data sets (CORINE Land Cover 2000 and the Block database) produced better models than each of the habitat datasets alone.

In Paper II, we used logistic regression to analyse the determinants of the presences/absences of Eurasian curlews on patches of farmland in a boreal region. In total 518 farmland patches were scanned for the presence of Eurasian curlews. Models based on patch characteristics, isolation measures and a number of geographical parameters (e.g. distance to nearest river) were compared by their AICc values in an information theoretical approach. Large and small scale auto-correlation was accounted for. The optimal model was then used to predict the effect of possible future changes in patch size and crop diversity on patch occupancy.

Paper III is based on numbers of foraging and non-foraging Eurasian curlews on 273 agricultural fields in northern Sweden during three periods of their breeding season. The observed distributions over agricultural treatment classes (ley, cereal, pasture and set-aside) were compared between periods and with random spatial distribution.

In Paper IV we analysed the effect of the construction of the Bothnia Line railway on the densities of Eurasian curlew and 12 other farmland breeding bird species. Nine years of 1823 ha territory mapping data from a before-during-after control-impact design were modelled in a mixed effects frame following the Zuur *et al.* (2009) protocol. Site and year were the potentially random effect variables, and railway construction (levels: before, during and after) and year the fixed effect variables.

For Paper V, we experimentally measured the flight initiation distances (FID) of incubating Eurasian curlews approached by a human observer. We tested the relation between FID and hatching success, and if FID was adjusted for date, time of the day and vegetation height. Finally, we analysed the consistency of FID measurements of individual nests.

4 Results

4.1 Paper I

Geographically, the Eurasian curlew had a more northern and eastern distribution than the northern lapwing. For both species, arable land was the CORINE Land Cover 2000 habitat class with the highest densities, followed by pastures (Table 1). Eurasian curlew densities on mires were 38% of those on arable land, but only 9% for northern lapwing. Northern lapwings were common in coastal habitats, but not near fresh water, while Eurasian curlew were strongly associated with human settlements and freshwater, but not with coastal habitat (Table 1). Based on the optimal habitat association models and the proportion of the habitats along SBS count transects, 17% of the Swedish Eurasian curlews were found on wetlands. The corresponding proportion for northern lapwing was 6%.

Eurasian curlew models were poor predictors of the abundances of northern lapwing, and *vice versa*. Finally, combining two independent habitat datasets produced better species-habitat association models than each of the datasets alone (Table 2).

Table 1. Predicted relative densities ($\text{density}_{\text{Arable}} = 100$) of Eurasian curlew and northern lapwing in CORINE Land Cover 2000 habitats included in the optimal models.

	Eurasian curlew	Northern lapwing
Arable	100	100
Pasture	61	51
Settlement	50	NA
Mire	38	9
Wetland	NA	4
Water	37	8
Sea	NA	41

Table 2. $AICc$ values of the empty model (without fixed effect variables) and $\Delta AICc$ between the empty model and optimal models based on various habitat datasets (transect data for 1999-2008, distance = 200 m).

Habitat dataset	Eurasian curlew	Northern lapwing
Empty model ($AICc$)	-24802	8217
CORINE ($\Delta AICc$)	-466	-2284
Block ($\Delta AICc$)	-390	-2389
CORINE + Block ($\Delta AICc$)	-519	-2436

4.2 Paper II

Patch size was the dominant predictor of presence of Eurasian curlew on farmland patches (Fig. 2), but crop heterogeneity and Easting + Easting² added additional explanatory power. A simulation test showed that the low occupancy rate on small patches (<11.5 ha) was not the result of sampling bias, but reflected ecological relevant differences exceeding the effect of acreage *per se*.

There was no difference between the river basins, and neither distances from the patch to the coast or the river, nor isolation measurements (proportions of non-farmland outside the patch within 0.5, 1, 2.5, 5 and 10 km respectively) added to model fit. No small scale spatial auto-correlation could be shown, but on a larger scale, occupancy rate increased towards the east, but peaked within the range of the study area.

The optimal model predicted that a 50% reduction of patch size would lead to a near to complete loss of occupied patches, while Eurasian curlews would be present on >2.5 times as many patches when patch size doubled (Fig. 3). An increase of crop heterogeneity could not compensate for area loss, but substantially increased occupancy levels when patch size was stable or increased (Fig. 3). The results of this study show that hindering shrinkage of patch size is an effective means to prevent local extinctions within a farmland habitat archipelago in a boreal landscape. Increased patch size may be a way to facilitate the expansion of Eurasian curlews, and probably even other farmland breeding bird species, within this fragmented habitat. The role of crop heterogeneity is less powerful, but mixing different crops within a farmland patch increases the chances that the patch will be occupied by breeding Eurasian Curlews.

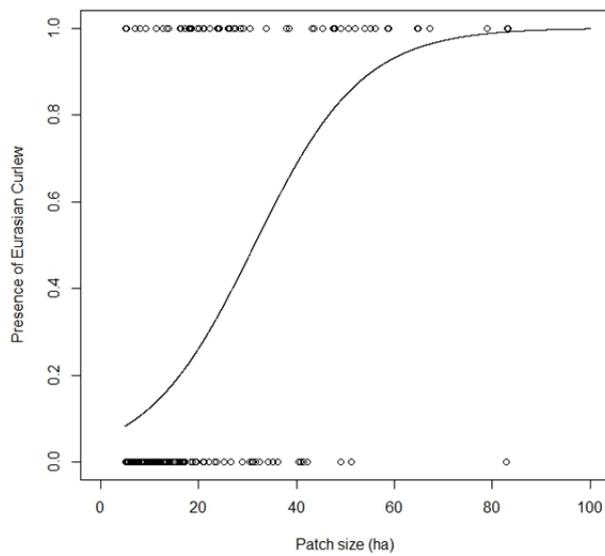


Figure 2. Area - presence relationship for medium sized (5 - 100 ha) farmland patches (N = 400) in the Ume and Vindel River drainage basins 2009. Circles mark observed presences and absences. The fitted incidence curve represents the predicted values according to the Area only generalized linear model. The 0.50 level of presence probability corresponds with an area of 31.4 ha.

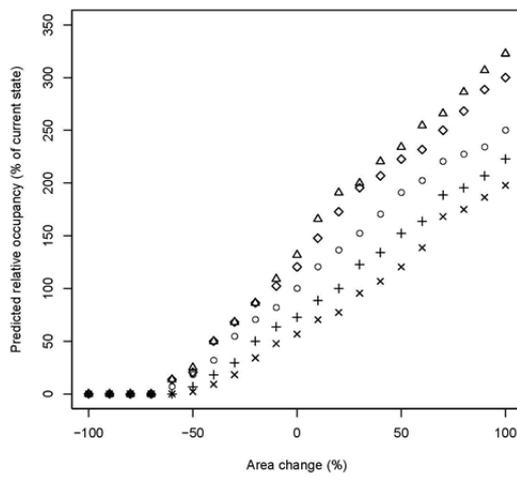


Figure 3. Predicted responses to changes in patch area and crop heterogeneity on the presences of Eurasian Curlews on farmland patches. All patches are assumed to change in relation to their current state (0% change) between total loss of farmland area (-100%) and doubling of patch area (+100%). Crop heterogeneity response: current status = circles, +1 crop type = diamonds, +2 = triangles, -1 = plus sign and -2 = crosses.

4.3 Paper III

More foraging Eurasian Curlews were observed on leys than expected from random spatial distribution during Period I (May 2-11) and II (May 26 – June 2), but less so in Period III (June 14-22), while on cereal fields the numbers were lower than expected during the first two periods, but much larger during the last (Fig. 4). This means that foraging Eurasian Curlews shifted from leys to cereal fields between Period II and III. Among the non-foraging birds there was a similar tendency, but the magnitude was much smaller. The differences were not related to proportions of male and females (males/females ratios 1.0, 1.3 and 1.5 for Period I-III respectively) and I argue that there was no significant exchange of the birds in the area during study period. Instead I suggest that the shift in foraging habitat was driven by prey accessibility, because soil living prey may have become harder to catch in untilled grassland soils compared to prey in loose soils of tilled cereal fields. For farmland bird conservation, my results imply that landscapes with leys and cereal fields are better breeding habitats than landscapes with only one of these treatment classes, because it allows the birds to choose the best foraging habitat when habitat quality changes over time.

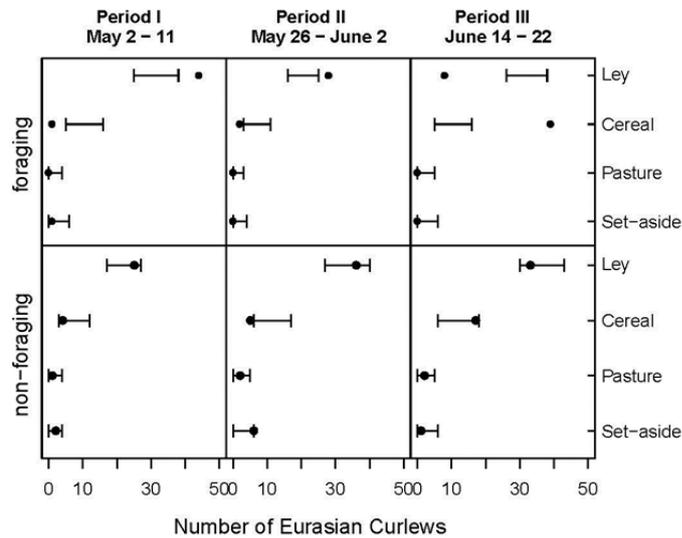


Figure 4. Observed numbers (dots) of foraging and non-foraging Eurasian Curlews over agricultural treatment classes and periods compared with 95% confidence intervals (CI's) under random spatial (binomial) distribution (bars). Observed numbers outside the 95% CI's indicate significantly ($P < 0.05$) lower or higher numbers than could be expected from chance alone.

4.4 Paper IV

For ten of the studied species, the treatment variable (coding for before, during and after railway construction) did not add significantly to model fit, and this means that no effect of railway construction could be demonstrated for these species (Table 3). Among the three species for which an effect of railway construction was found, the Eurasian skylark was affected negatively and little ringed plover and yellow wagtail positively. The densities of Eurasian curlew were not affected by railway construction, but showed a negative trend over the study period. The estimate of this trend corresponded with a 3% year⁻¹ decrease.

Table 3. Applied variance structures, included fixed and random effects, and random effect variance components in optimal mixed-effects models selected according Zuur et al. (2009). The treatment variable describes the conditions Before, During and After the construction of the Bothnia Line for the 19 studied sites. Response variable: yearly number of territories 100 ha⁻¹ (2002-2009). Mixed-effects models for common rosefinch did not converge

Species	Variance structure (varIdent)		Included effects		Random effect variance components (%)		
	Treatm.	Year	Fixed	Random	Site	Year	Resid.
Barn swallow	+	-	-	year,site	84	<1	16
Common rosefinch	+	+	-	-	-	-	-
Common snipe	-	+	-	site	63	-	37
Common starling	+	+	-	site	24	-	76
Eurasian curlew	-	-	year	year,site	78	<1	21
Eurasian skylark	-	-	Treatm.*year	year,site	92	<1	7
Green sandpiper	+	+	-	site	2	-	98
Little ringed plover	+	-	Treatm.	site	20	-	80
Meadow pipit	+	-	-	year,site	84	<1	15
Northern lapwing	-	-	-	year,site	86	<1	13
Red-backed shrike	+	-	-	year,site	77	5	18
Yellow wagtail	-	+	Treatm.*year	year,site	85	<1	14
Whinchat	-	-	-	site	56	-	44

4.5 Paper V

Nests where the incubation adult left at intermediate distances had a greater chance to hatch successfully compared with nests where the bird left at short or long distances (Fig. 5). Date and time of the evening correlated negatively with FID, which means that incubating parents let the intruder come closer before leaving the nest as the breeding season and the evening progressed. Finally, FID measurements from first, second and third nest visits were not correlated (Fig. 6).

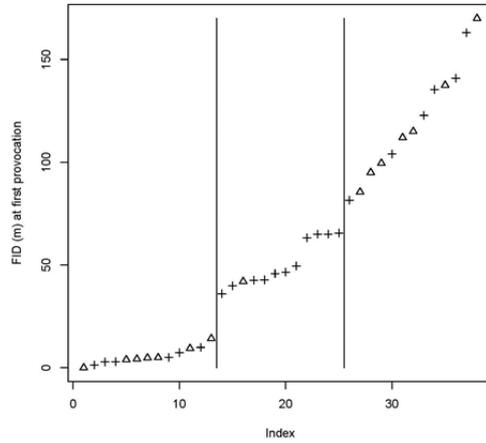


Figure 5. Ordered FID values at first provocation. Successfully hatched nest: +, failed nest: Δ . Vertical lines mark the borders between the three FID classes: short (n=13), medium (n=12) and long (n=13).

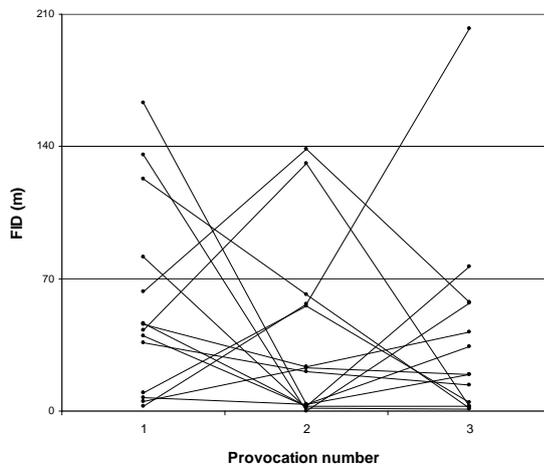


Figure 6. FID measurements from nests with three provocations. All nests except one hatched successfully.

5 Discussion

5.1 Eurasian curlew and northern lapwing habitat associations

Productivity, ambient energy and hydrology are among the factors determining species abundances at continent scale (e.g. Stefanescu *et al.*, 2011; Carnicer & Diaz-Delgado, 2008). The Species Temperature Index (average summer temperature of the European breeding range) for Eurasian curlew (12.0°C) and northern lapwing (13.6°C) are the result of such factors (Devictor *et al.*, 2008) and could partially explain the different effects of Northing and Easting observed in Paper I.

At the national level, the models in Paper I confirm the role of farmland and wetlands (including coastal habitats) for the abundances of both species (Table 1), but the relative importance of these habitat types differed between the species. The coastal association in northern lapwing may be related to the westerly distribution of the species throughout the Western Palearctic (Cramp, 1983) compared with the Eurasian curlew. This Eurasian curlew was not significantly associated with coastal habitats, but strongly so with freshwater and wetland habitats. The association with human settlements expressed in Eurasian curlew models is probably caused by the association between farmland and villages and towns in northern Sweden, where this species is most common (Svensson *et al.*, 1999; Fig. 1). In these landscapes, farmland is seldom found far from villages and towns (Digital map of Sweden, <http://www.lantmateriet.se>). Thus, the association with settlements could be added to the farmland association aspect.

The weak association with wetlands expressed in the northern lapwing models contrasts with the Swedish breeding habitat description in Svensson *et al.* (1999), while our findings correspond well with the European habitat description in del Hoyo *et al.* (1996). Contrastingly, this latter source stresses the importance of wet habitats for Eurasian curlews, while Svensson *et al.*

(1999) emphasizes the role of farmland. These examples seem to illustrate the spatio-temporal dynamics of habitat association.

Despite the similarities between the optimal models for the two species (Paper I), models for one species were poor predictors of the abundances of the other species. In an era of meta-analyses (e.g. Benitez-Lopez *et al.*, 2010; Riffell *et al.*, 2011; Ibanez-Alamo *et al.*, 2012) and multispecies indicators (e.g. Gregory *et al.*, 2008; Gregory *et al.*, 2009; Gregory & van Strien, 2010), there seems to be a risk for single species based models to be applied on data for other species or species-clusters (c.f. Jetz, 2012). Our results show that this could lead to faulty predictions, even when the species appear to be ecologically similar.

5.2 Models based on multiple habitat data sets

The major novelty of the Akaike Information Criterion (Akaike, 1974) was the introduction of a penalty for each added coefficient (variable) to counteract tendencies to over-parameterize explanatory models. Meanwhile, the complex nature of ecological systems makes adding more explanatory variables a tempting option in many modelling situations. The continuous increase in the number of large-scale systematic bird surveys (e.g. Gregory *et al.*, 2005; Gregory *et al.*, 2009), paralleled by an increased availability of large-scale high-quality habitat data (Guisan & Thuiller, 2005), provide ever increasing opportunities to model and evaluate the occurrence and fate of breeding birds in relation to their habitat requirements. The positive results of our test to combine two different land use datasets (Paper I) suggest that adding more explanatory information can be fruitful.

The main shortcoming of the CORINE Land Cover 2000 dataset was its invariability over time. In the future, regular updates of the Swedish CORINE Land Cover will be available, but no yearly updates are planned (Eionet EAGLE initiative, <http://sia.eionet.europa.eu/EAGLE/#Description>). The main strength of the Block habitat database was that the habitat information was updated yearly. Unfortunately, the data were basically prognoses for coming land-use under an imperfect update and control scheme. Ideally, the future Block database should also include time-stamped information about activities that change the ecological function of agricultural fields, e.g. tilling and harvesting.

For the future, the habitat dataset of our choice would a) be yearly updated to describe the conditions during the breeding season, b) be based on a “smarter” classification system, c) have very high spatial resolution, and d) contain other ecologically relevant features than land cover. For studies of

farmland breeding bird species, non-polygon features (e.g. open ditches, hedgerows, agricultural buildings, stone walls, solitary trees) are likely to have high explanatory potential (e.g. Ståhl *et al.*, 2011). Among other data sources for habitat association modelling, high resolution elevation data (e.g. the new LIDAR based digital elevation model of Sweden) appear to have special potential. In addition to being potentially explanatory (expressed in e.g. slope or exposition), elevation data may be used to adjust the bird data for detectability. In addition to the improvement of habitat data, future species distribution models will probably include species interactions (e.g. Campomizzi *et al.*, 2008), soil physics, behaviour and personality (Sih *et al.*, 2012; Gordon, 2011), and could largely be based on long-term monitoring of individual animals (Bunnefeld *et al.*, 2011).

5.3 Importance of patch size

For long-lived, highly mobile, migratory species, meta-population theory (Hanski, 1994; Gill, 1978) is unlikely to be a good predictor of patch occupancy at landscape scale. In these species, a breeding habitat patch is “immigrated” at the return of each migration (c.f. Bowman *et al.*, 2002) as a result of an evaluation process, usually including a number of alternative patches. Available resources, perceived predation risk, interactions with conspecifics and experience will be important components in this evaluation process (e.g. Campomizzi *et al.*, 2008; Whittingham *et al.*, 2006).

If one or more of these factors relate to patch size, a “desertion threshold”, analogous to an extinction threshold (Fahrig, 2002), can be expected. For example, predation risk has been shown to correlate negatively with patch size (Reino *et al.*, 2009; Morris & Gilroy, 2008). When a patch is too small to provide sufficient breeding habitat conditions, it will not be colonized for the season, and when unoccupied patches are available in the neighbourhood, these will be used instead.

The Eurasian curlew is an interior species with respect to farmland patches in a boreal matrix, and according to the meta-analysis by Bender *et al.* (1998) a strong effect of patch size on occupancy rate can be predicted. The effect of patch size reduction shown for this species in Paper II is in line with this prediction. Also, the size effect in Paper II could not be attributed to sampling bias, because the simulation program produced a patch occupancy rate of 27 for aggregations of small patches compared with a >50% rate for single patches of similar size. The additional effect of within-patch number of crops that we describe (Paper II) is in concordance with the positive effects of

agricultural landscape heterogeneity on species occurrence demonstrated by Benton *et al.* (2003) and Fahrig *et al.* (2011).

Considering that the Ume and Vindel River basins are strongholds of the species in Sweden (de Jong & Berg, 2001), landscape transformations that cause the loss of relatively large patches could have regional conservation consequences. Responses to changes in patch area and crop diversity predicted by the optimal model in Paper II (Fig. 3) stress the importance of active agriculture in the boreal landscape for the distribution of the Eurasian Curlew. The model suggests that a further reduction of farming on marginal lands quickly reduces the number of patches occupied by the species, and that these local extinctions are likely to amalgamate to regional extinctions. The driving forces are reduced acreage of suitable habitat, and to a lesser degree, loss of crop heterogeneity. Agriculture is highly governed by central policy decisions and subsidies. For decades, these have driven farming towards specialization, intensification and concentration. In the county Västerbotten, where the study area is situated, total area of arable and fallow land decreased with 42% since 1951 (Statistics Sweden, www.scb.se). According to the model of Paper II (Fig. 3), a reduction of that size would have caused a >80% reduction of occupied farmland patches within the region of our study. This level of reduction would occur if all patches were reduced proportional. If this reduction was applied on small patches only, the loss of occupancy would be less (these patches seldom had any Eurasian curlews to loose), but if the area reduction concentrated on the 20-50 ha sized patches, the losses would probably be substantially larger. Conservation of the Eurasian curlew, and probably several other farmland breeding species, would benefit greatly from redirecting support from users of small patches to users of larger (approximately >20 ha) patches. Special focus should be set on enlarging mid-sized patches, while supporting farming of large (>100 ha) patches would be less cost-effective.

5.4 Foraging habitat shift

Based on the marginal value theorem (Charnov, 1976) and Oaten's (1977) optimal foraging strategy under stochastic processes, Green (1980) proposed a Bayesian behaviour model, where the quality of the current location is evaluated continuously. McNamara (1982) applied this on stochastic environments distributed in well-defined patches, where the decision to continue foraging or to move to the next location is made on the patch level. Later McNamara and Houston (1985) added the process of learning (and thus experience) to these optimal foraging models.

The Eurasian curlews in Paper III were breeding birds within territories made up by an aggregation of agricultural fields. Although the land-use and location of these fields remained the same over the study period, their characteristics changed due to management, vegetation growth and climatic processes. I assumed that the same birds were present throughout the study, because the study period fell between migration periods. The lack of differences between periods in total numbers, the sex ratio and the proportion foraging birds support this assumption. Given the breeding site fidelity of adults (Cramp, 1983) and the long life-expectancy of the species (Fransson *et al.*, 2008), most of the birds were non-naïve in respect of their breeding habitat. For the purpose of this study, I classified behaviour into “foraging” and “non-foraging”, but each bird changes between these behavioural classes multiple times per day, and thus all birds belonged to the same sample.

In this setting, I found that foraging birds reversed their preference of leys over cereal fields during the second half of June (Fig. 4). Non-foraging birds were distributed over field classes in a way that did not differ ($P>0.05$) from random spatial distribution. My conclusion is that the relative quality of leys and cereal fields as foraging habitat changed, while this change was not important for birds that were not busy foraging. It seems likely that experienced Eurasian curlews can recognize fields as a habitat patch unit, and use this entity in their foraging habitat decision (the omniscient strategy in Green, 1980), but the observed foraging habitat shift could also have arisen from naïve, but spatially auto-correlated sampling by the foraging birds.

Changes in habitat quality for foraging may have been related to prey density (but see Berg, 1993), perceived predation risk (e.g. Whittingham & Evans, 2004), ease of locomotion, prey detectability (Devereux *et al.*, 2004) or prey accessibility (Finn *et al.*, 2008). I suggest that soil penetrability was an important driver of the foraging habitat shift, because the soils of cereal fields were loose as a result of tilling, so that soil-living prey could be reached more easily than in untilled soils.

Landscape heterogeneity is increasingly recognized as an important factor in maintaining farmland biodiversity (Benton *et al.*, 2003; Herzon & O’Hara, 2007). Due to its multiple dimensions and scales, the concept of landscape heterogeneity is complex, and the links between heterogeneity components and biodiversity are only partially understood (Tschardtke *et al.*, 2005; Fahrig *et al.*, 2011). Nevertheless, various heterogeneity-based farmland bird conservation measures have already earned their merits (Wilson *et al.*, 2005; Schekkerman *et al.*, 2008), but these measures reduce crops and increase costs, and thus rely on financial compensation to farmers. My results indicate that mixing commercially managed crops in a medium grained agricultural

landscape may enhance choice and hence overall foraging habitat quality for Curlews. Conservation measures based on increasing heterogeneity by commercial management should be relatively cheap to implement and easily accepted by farmers.

5.5 Railway construction and farmland birds

Roads and railways are generally thought to have a negative impact on wildlife populations (Fahrig & Rytwinski, 2009), and in a recent meta-analysis Benitez-Lopez *et al.* (2010) summarized the impact level in single models for mammals and birds. Most of the underlying studies compared densities near infrastructure with densities far enough to be considered unaffected, a control-impact design (e.g. Reijnen *et al.*, 1996; Forman *et al.*, 2002). The major drawbacks of this design are that (a) the original state of the wildlife population is unknown, and (b) all possible mechanisms by which infrastructure could affect wildlife are integrated and summed up over time. Fahrig & Rytwinski (2009) proposed before-after control-impact studies to solve these two problems and Roedenbeck *et al.* (2007) extended the concept into a before-during-after control-impact (BDACI) design. The BDACI study of the construction of the Bothnia Line and farmland breeding birds In Paper IV was started with a pilot study in 2000.

The mechanisms by which roads and railways could affect wildlife can be grouped into (a) habitat alteration, (b) barrier effects, (c) mortality and (d) disturbance (Spellerberg, 1998; Trombulak & Frissell, 2000). Of these, mortality and disturbance are mainly associated with traffic. Disturbance by traffic noise has received much attention (Reijnen *et al.*, 1997; Francis *et al.*, 2009; Parris & Schneider, 2009), but its importance has recently been by Summers *et al.* (2011).

Multiple sites, multiple year BDACI studies produce data with potentially random effects of site (random intercept) and year (random slope). Such data are adequately handled in a mixed-effects framework (Pinheiro & Bates, 2000).

From the lack of negative impact observed in Paper IV (Table 4), we conclude that a general negative effect of infrastructure on birds (*sensu* Benítez-López *et al.*, 2010) is related to traffic related mechanisms rather than to railway construction *per se*. For birds in open landscapes, it seems unlikely to expect a significant barrier effect of a railway. The positive effects signal that there is potential for deliberately create (and manage) favourable habitats for birds in connection with infrastructure construction. These findings can be

used to plan cost-effective mitigation and offset programs for large infrastructure project (McKenney *et al.*, 2010).

5.6 FID and hatching success

Nests of waders are subject for high predation pressure (Berg, 1992; Currie *et al.*, 2001; MacDonald & Bolton, 2008) and consequently, parent behaviour that reduces predation risk are likely to have a major impact on overall fitness (Montgomerie & Weatherhead, 1988); Lima, 2009). Eurasian curlews, like most waders, are ground-nesting and unable to cover their eggs at nest departure. Consequently the only behavioural options for nest defence are (a) nest site selection, (b) vigilance (c.f. Cooper, 2008), (c) flight initiation distance (FID), and (d) distractive or aggressive behaviour versus the predator.

A trade-off between the survival of the parent and the protection of the eggs may not fully describe the components of the FID cost-benefit analysis. For example, if the eggs are better camouflaged than the adult or the smell of the adult guides the predator to the nest, leaving the nest early may be advantageous for the eggs. The optimal FID models proposed by Cooper & Frederick (2007) can incorporate such additional factors, but by doing so, the graphical approach to predict FID (Ydenberg & Dill, 1986) collapses. The complexity of the cost-benefit decision may explain why the observed FID's in Paper V showed substantial variation (Fig. 5). In the light of this variation, the effects of date and time of the evening (2.4 m day^{-1} and 0.5 m h^{-1}) were moderate. The effect of date is likely to be related to the increasing relative value of the current clutch as the breeding season progresses (Biermann & Robertson, 1981), while the effect of time may be related to the increasing need to brood the eggs (Camfield & Martin, 2009) when ambient temperatures drop during the course of the evening.

Evolutionary stable strategy theory (Maynard Smith & Price, 1973) could explain why the results of Paper V show that nests with medium long FID had higher hatching success than nests where the incubating parent left early or late (Fig. 5). If fleeing immediately came at no costs, natural selection would have favoured this behaviour, and if staying came at no costs, selection would favour birds that stayed on the nest “until the bitter end”. With costs and benefits for both staying and leaving, intermediate FID would develop into the evolutionary stable strategy.

The tests for consistency in FID between provocations (Fig. 6) indicated that there is no individuality in the response to the approaching observer, neither at a stable level, nor as a consistent trend. We propose a “surprise” strategy to explain this lack in consistency in FID, and suggest that this

strategy can be beneficial for the adult, the eggs or both, because it prevents predators from learning how to interpret the behaviour of incubating birds.

5.7 Conclusions and applications

In times when Western world citizens are swamped by decisions about healthy food (Grunert & Wills, 2007), care for the environment (D'Souza *et al.*, 2007) or pocket-money (Xavier, 2008), it can be wise to reflect upon the decision-making environment of animals. For humans, suboptimal choices may be punished by an extra BMI score, bad conscience or getting less rich. For animals an empty stomach, loss of offspring or life may be at stake. Maybe we should care less about consumption and more about how we influence the options of the fellow inhabitants of the world. We have the choice!

Predictive models can help us make wise choices. Modelling techniques can and must be taken much further than the ones presented in this thesis, but it is crucial to keep focused on the quality of the data on which the models are built. Here I would like to pay homage to all those field-ornithologist who spend their time (often unpaid for) systematically collecting the data that allow us to make informed decisions for our common future.

For a next step in the development of habitat association models based on the national bird survey data, I suggest repeated models based on matching time periods for the bird and habitat data. The parameters of these models could then be averaged or analysed for trends. Preferably, these models are made on a yearly basis (e.g. for SBS and Block data), but even models based on multiple year periods could be fruitful. Additional environmental data would also help to improve the models.

The design of data collection schemes and the interpretation of modelling results are highly dependent on thorough autecological knowledge of the species involved. This knowledge can seldom be achieved without long-term studies of various aspects of the life of the species. The current trend to concentrate scientific effort on a small number of model species should not come at the cost of a serious lack of knowledge of other species. In depth species-specific knowledge will also enable us to integrate behavioural ecology (e.g. Gordon, 2011) and individual variation (e.g. Sih *et al.*, 2012) into the predictive models. This effort will be aided by the results of large scale, long-term tracking of individual animals (c.f. Bunnefeld *et al.*, 2011).

Conservation of the declining Eurasian curlew population has been an important motive behind the studies in this thesis. The results suggest the following applications:

- Sufficiently large farmland patches in boreal landscapes should be conserved or created, especially in the core areas of the distribution of Eurasian curlew. Subsidies to farmers could be used to reach this goal.
- Eurasian curlews seem to benefit from having access to both grasslands and cereal (tillage) fields within their home range during the breeding season. Again, subsidies could be used to deliver these conditions.

The home of farmland breeding birds was shaped by humans, and can be made hostile or hospitable by the choice of humans. When given adequate options to choose from, Eurasian curlews are likely be able to match their changing world.

6 References

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19 (6): 716–723
- Anderson, G.Q.A., Bradbury, R.B. & Evans, A.D. (2001). Evidence for the effects of agricultural intensification on wild bird populations in the UK. *RSPB Research Report* 3, 1-44.
- Antonsson, H. & Jansson, U. (eds.) (2011). *Jordbruk och skogsbruk i Sverige sedan år 1900 - studier av de areella näringarnas geografi och historia*. Skogs- och lantbrukshistoriska meddelanden nr 53. Kungliga skogs- och lantbruksakademien, Stockholm, Sweden. [In Swedish]
- Aranzabal, I., Schmitz, M.F., Aquilera, P. & Pineda, F.D. (2008). Modelling of landscape changes derived from the dynamics of socio-ecological systems - A case of study in a semiarid Mediterranean landscape. *Ecological Indicators* 8(5), 672-685.
- Austin, M.P. (2002). Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157(2-3), 101-118.
- Battin, J. (2004). When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Conservation Biology* 18(6), 1482-1491.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters* 15(4), 365-377.
- Bender, D.J., Contreras, T.A. & Fahrig, L. (1998). Habitat Loss and Population Decline: A Meta-Analysis of the Patch Size Effect. *Ecology* 79(2), 517-533.
- Benítez-López, A., Alkemade, R. & Verweij, P.A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation*, 143, 1307-1316.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution* 18(4), 182-188.
- Berg, Å. (1992). Factors affecting nest-site choice and reproductive success of Curlews *Numenius arquata* on farmland. *Ibis* 134: 44-51.
- Berg, Å. (1993). Food resources and foraging success of curlews *Numenius arquata* in different farmland habitats. *Ornis fennica* 70(3): 22-31.
- Biermann, G.C. & Robertson, R.J. (1981). An increase in parental investment during the breeding season. *Animal Behaviour* 29(2), 487-489.

- Bock, C.E. & Jones, Z.F. (2004). Avian Habitat Evaluation: Should Counting Birds Count? *Frontiers in Ecology and the Environment* 2(8), 403-410.
- Bowman, J., Cappuccino, N. & Fahrig, L. (2002). Patch size and population density: the effect of immigration behavior. *Conservation Ecology* 6(1).
- Bunnefeld, N., Boerger, L., van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J. & Ericsson, G. (2011). A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* 80(2), 466-476.
- Camfield, A.F. & Martin, K. (2009). The influence of ambient temperature on horned lark incubation behaviour in an alpine environment. *Behaviour* 146, 1615-1633.
- Campomizzi, A.J., Butcher, J.A., Farrell, S.L., Snelgrove, A.G., Collier, B.A., Gutzwiller, K.J., Morrison, M.L. & Wilkins, R.N. (2008). Conspecific attraction is a missing component in wildlife habitat modeling. *Journal of Wildlife Management* 72(1), 331-336.
- Carnicer, J. & Diaz-Delgado, R. (2008). Geographic differences between functional groups in patterns of bird species richness in North America. *Acta Oecologica-International Journal of Ecology* 33(2), 253-264.
- Charnov, E.L. (1976). Optimal foraging: the marginal value theorem. *Theoretical Population Biology* 9: 129-136.
- Cooper, W.E. & Frederick, W.G. (2007). Optimal flight initiation distance. *Journal of Theoretical Biology* 244: 59-67.
- Cooper, W.E., Jr. (2008). Visual monitoring of predators: occurrence, cost and benefit for escape. *Animal Behaviour* 76, 1365-1372.
- Cramp, S. (Ed.) (1983). *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic*. Vol. III. Oxford University Press, Oxford, UK.
- Currie, D., Valkama, J., Berg, Å., Boschert, M., Norrdahl, Hänninen, M., Korpimäki, E., Pöyri, V. & Hemminki, O. (2001). Sex roles, parental effort and offspring desertion in the monogamous Eurasian Curlew *Numenius arquata*. *Ibis* 143: 642-650.
- D'Souza, C., Taghian, M., Lamb, P. & Peretiatko, R. (2007). Green decisions: demographics and consumer understanding of environmental labels. *International Journal of Consumer Studies* 31(4), 371-376.
- Darwin, C. (1859). *On the origin of species*. John Murray, London.
- Davey, C.M., Vickery, J.A., Boatman, N.D., Chamberlain, D.E., Parry, H.R. & Siriwardena, G.M. (2010). Assessing the impact of Entry Level Stewardship on lowland farmland birds in England. *Ibis* 152(3), 459-474.
- de Jong, A. & Berg, Å. (2001). Storspoven i Sverige. Resultat av riksinventeringen 1999. *Vår Fågelvärld* 60(2): 6-16. [In Swedish]
- del Hoyo, J., Elliott, A. & Sargatal, J. (Eds.) (1996). *Handbook of the Birds of the World. Vol. 3*. Lynx Edicions, Barcelona.
- Devereux, C.L., McKeever, C.U., Benton, T.G. & Whittingham, M.J. (2004). The effect of sward height and drainage on Common Starlings *Sturnus vulgaris* and Northern Lapwings *Vanellus vanellus* foraging in grassland habitats. *Ibis* 146, 115-122.
- Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society London B* 275, 2743-2748.

- Dirk, S. (2005). Marginal lands in Europe—causes of decline. *Basic and Applied Ecology* 6(2), 99-106.
- Elith, J. & Leathwick, J.R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology Evolution and Systematics*. 40: 677-697.
- Fahrig, L. & Rytwinski, T. (2009). Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society*, 14, 21.
- Fahrig, L. (2002). Effect of Habitat Fragmentation on the Extinction Threshold: A Synthesis. *Ecological Applications* 12(2), 346-353.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* 14(2), 101-112.
- Finn, P.G., Catterall, C.P. & Driscoll, P.V. (2008). Prey versus substrate as determinants of habitat choice in a feeding shorebird. *Estuarine Coastal and Shelf Science* 80(3), 381-390.
- Forman, R.T.T., Reineking, B. & Hersperger, A.M. (2002). Road traffic and nearby grassland bird patterns in a suburban landscape. *Environmental Management*, 29, 782-800.
- Francis, C.D., Ortega, C.P. & Cruz, A. (2009). Noise pollution changes avian communities and species interactions. *Current Biology*, 19, 1415-1419.
- Fransson, T., Österblom, H. & Hall-Karlsson, S. (2008). [*Swedish Bird Ringing Atlas*, Vol 2.] Stockholm. [In Swedish with English summary]
- Gill, D.E. (1978). Meta-population ecology of red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* 48(2), 145-166.
- Gill, R.E., Jr., Piersma, T., Hufford, G., Servranckx, R. & Riegen, A. (2006). *Crossing the ultimate ecological barrier: evidence for an 11 000 km long non-stop flight from Alaska to New Zealand and eastern Australia by bar-tailed godwits Limosa lapponica*. (Waterbirds around the world: a global overview of the conservation, management and research of the world's waterbird flyways. International conference on waterbirds held in Edinburgh in April 2004. ISBN 0-11-497333-4.
- Gilroy, J.J., Anderson, G.Q.A., Grice, P.V., Vickery, J.A. & Sutherland, W.J. (2010). Mid-season shifts in the habitat associations of Yellow Wagtails *Motacilla flava* breeding in arable farmland. *Ibis* 152(1), 90-104.
- Gilroy, J.J., Anderson, G.Q.A., Vickery, J.A., Grice, P.V. & Sutherland, W.J. (2011). Identifying mismatches between habitat selection and habitat quality in a ground-nesting farmland bird. *Animal Conservation* 14(6), 620-629.
- Gordon, D.M. (2011). The fusion of behavioral ecology and ecology. *Behavioral Ecology* 22(2), 225-230.
- Green, R.F. (1980). Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. *Theoretical Population Biology* 18: 244-256.
- Gregory, R.D. & van Strien, A. (2010). Wild bird indicators: using composite population trends of birds as measures of environmental health. *Ornithological Science* 9(1), 3-22.
- Gregory, R.D., Noble, D.G. & Custance, J. (2004). The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis* 146, 1-13.

- Gregory, R.D., van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., et al. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B-Biological Sciences* 360, 269–288.
- Gregory, R.D., Willis, S.G., Jiguet, F., Vorisek, P., Klvanova, A., van Strien, A., Huntley, B., Collingham, Y.C., Couvet, D. & Green, R.E. (2009). An Indicator of the Impact of Climatic Change on European Bird Populations. *Plos One* 4(3).
- Gregory, R.D., Vorisek, P., Noble, D.G., Van Strien, A., Klvanova, A., Eaton, M., Meyling, A.W.G., Joys, A., Foppen, R.P.B. & Burfield, I.J. (2008). The generation and use of bird population indicators in Europe. *Bird Conservation International* 18, S223-S244.
- Grunert, K. & Wills, J. (2007). A review of European research on consumer response to nutrition information on food labels. *Journal of Public Health* 15(5), 385-399.
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8(9), 993-1009.
- Hanski, I. (1994). Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology & Evolution* 9(4), 131-135.
- Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R.F.A., Niemelä, J., Rebane, M., Wascher, D., Watt, A. & Young, J. (2008). Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe—A review. *Agriculture, Ecosystems and Environment* 124(1–2), 60-71.
- Herzon, I. & O'Hara, R.B. (2007). Effects of landscape complexity on farmland birds in the Baltic States. *Agriculture, Ecosystems and Environment* 118: 297-306.
- Ibanez-Alamo, J.D., Sanllorente, O. & Soler, M. (2012). The impact of researcher disturbance on nest predation rates: a meta-analysis. *Ibis* 154(1), 5-14.
- Jetz, W., McPherson, J.M. & Guralnick, R.P. (2012). Integrating biodiversity distribution knowledge: toward a global map of life. *Trends in Ecology and Evolution* 27(3): 151-159.
- Kleijn, D., Kohler, F., Baldi, A., Batary, P., Concepcion, E.D., Clough, Y., Diaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovacs, A., Marshall, E.J.P., Tscharntke, T. & Verhulst, J. (2009). On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society B-Biological Sciences* 276(1658), 903-909.
- Kleijn, D., Rundlof, M., Scheper, J., Smith, H.G. & Tscharntke, T. (2011). Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution* 26(9), 474-481.
- Lima, S.L. (2009). Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews* 84: 485-513.
- Lindström, A., Green, M. & Ottvall, R. (2012). *Monitoring population changes of birds in Sweden. Annual report for 2011*. Department of Biology, Lund University, Sweden. 82 pp.
- MacDonald, M.A. & Bolton, M. (2008). Predation on wader nests in Europe. *Ibis* 150, 54-73.
- Mattison, E.H.A. & Norris, K. (2005). Bridging the gaps between agricultural policy, land-use and biodiversity. *Trends in Ecology & Evolution* 20(11), 610-616.
- Maynard Smith, J. & Price, G.R. (1973). The logic of animal conflict. *Nature* 246(5427): 15-18.
- McKenney, B.A. & Kiesecker, J.M. (2010). Policy development for biodiversity offsets: a review of offset frameworks. *Environmental Management* 45, 165-176.

- McNamara, J. (1982). Optimal patch use in a stochastic environment. *Theoretical Population Biology* 21: 269-288.
- McNamara, J.M. & Houston, A.I. (1985). Optimal foraging and learning. *Journal of Theoretical Biology* 117(2), 231-249.
- Mehra, J. & Rechenberg, H. (1982). *The historical development of quantum theory*, Springer-Verlag, New York, USA.
- Miguel, A. (1999). The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems & Environment* 74(1-3), 19-31.
- Montgomerie, R.D. & Weatherhead, P.J. (1988). Risks and rewards of nest defense by parent birds. *Quarterly Review of Biology* 63(2), 167-187.
- Morris, A.J. & Gilroy, J.J. (2008). Close to the edge: predation risks for two declining farmland passerines. *Ibis* 150, 168-177.
- Newton, I. (2004). The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146(4), 579-600.
- Oaten, A. (1977). Optimal foraging: the marginal value theorem. *Theoretical Population Biology* 12: 129-136.
- O'Brien, M. & Wilson, J.D. (2011). Population changes of breeding waders on farmland in relation to agri-environment management. *Bird Study* 58(4), 399-408.
- Parris, K.M. & Schneider, A. (2009). Impacts of traffic noise and traffic volume on birds of roadside habitats. *Ecology and Society* 14, 29.
<http://www.ecologyandsociety.org/vol14/iss1/art29/>. Accessed 19 Sept 2011
- Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12(5), 361-371.
- Pinheiro, J.C. & Bates, D.M. (2000). *Mixed-effects models in S and S-PLUS*. Springer Verlag. New York.
- Pärt, T., Arlt, D. & Villard, M.-A. (2007). Empirical evidence for ecological traps: a two-step model focusing on individual decisions. *Journal of Ornithology* 148, S327-S332.
- Reed, T.E., Schindler, D.E. & Waples, R.S. (2011). Interacting Effects of Phenotypic Plasticity and Evolution on Population Persistence in a Changing Climate. *Conservation Biology* 25(1), 56-63.
- Reijnen, R., Foppen, R. & Meeuwsen, H. (1996). The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biological Conservation*, **75**, 255-260.
- Reijnen, R., Foppen, R. & Veenbaas, G. (1997). Disturbance by traffic of breeding birds: evaluation of the effect and considerations in planning and managing road corridors. *Biodiversity and Conservation*, **6**, 567-581.
- Reino, L., Beja, P., Osborne, P.E., Morgado, R., Fabiao, A. & Rotenberry, J.T. (2009). Distance to edges, edge contrast and landscape fragmentation: Interactions affecting farmland birds around forest plantations. *Biological Conservation* 142(4), 824-838.
- Remes, V. (2000). How can maladaptive habitat choice generate source-sink population dynamics? *Oikos* 91(3), 579-582.

- Rhymer, C.M., Robinson, R.A., Smart, J. & Whittingham, M.J. (2010). Can ecosystem services be integrated with conservation? A case study of breeding waders on grassland. *Ibis* 152(4), 698-712.
- Riffell, S., Verschuyf, J., Miller, D. & Wigley, T.B. (2011). A meta-analysis of bird and mammal response to short-rotation woody crops. *Global Change Biology Bioenergy* 3(4), 313-321.
- Robertson, G.A. & Hutto, R.L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87(5), 1075-1085.
- Roedenbeck, I.A., Fahrig, L., Findlay, C.S., Houlihan, J.E., Jaeger, J.A.G., Klar, N., Kramer-Schadt, S. & van der Grift, E.A. (2007). The Rauschholzhausen Agenda for road ecology. *Ecology and Society*, 12, 11. <http://www.ecologyandsociety.org/vol12/iss1/art11/>. Accessed 19 Sept 2011.
- Sahlsten, J., Bunnefeld, N., Mansson, J., Ericsson, G., Bergstrom, R. & Dettki, H. (2010). Can supplementary feeding be used to redistribute moose *Alces alces*? *Wildlife Biology* 16(1), 85-92.
- Schekkerman, H., Teunissen, W. & Oosterveld, E. (2008). The effect of “mosaic management” on the demography of black-tailed godwit *Limosa limosa* on farmland. *Journal of Applied Ecology* 45: 1067-1075.
- Schmidt, K.A., Dall, S.R.X. & van Gils, J.A. (2010). The ecology of information: an overview on the ecological significance of making informed decisions. *Oikos* 119(2), 304-316.
- Seppanen, J.-T., Forsman, J.T., Monkkonen, M. & Thomson, R.L. (2007). Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* 88(7), 1622-1633.
- Sih, A., Cote, J., Evans, M., Fogarty, S. & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters* 15(3), 278-289.
- Smith, B.R. & Blumstein, D.T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* 19(2), 448-455.
- Spellerberg, I.F. (1998). Ecological effects of roads and traffic: a literature review. *Global Ecology and Biogeography*, 7, 317-333.
- Stefanescu, C., Carnicer, J. & Penuelas, J. (2011). Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. *Ecography* 34(3), 353-363.
- Ståhl, G., Allard, A., Esseen, P.-A., Glimskär, A., Ringvall, A., Svensson, J., Sundquist, S., Christensen, P., Gallegos Torell, Å., Högström, M., Lagerqvist, K., Marklund, L., Nilsson, B. & Inghe, O. (2011). National Inventory of Landscapes in Sweden (NILS) - scope, design, and experiences from establishing a multiscale biodiversity monitoring system. *Environmental Monitoring and Assessment* 173,579-595.
- Summers, P.D., Cunningham, G.M. & Fahrig, L. (2011). Are the negative effects of roads on breeding birds caused by traffic noise? *Journal of Applied Ecology*, 48, 1527-1534.
- Sutherland, W.J., Aveling, R., Bennun, L., Chapman, E., Clout, M., Côté, I.M., Depledge, M.H., Dicks, L.V., Dobson, A.P., Fellman, L., Fleishman, E., Gibbons, D.W., Keim, B., Lickorish, F., Lindenmayer, D.B., Monk, K.A., Norris, K., Peck, L.S., Prior, S.V., Scharlemann, J.P.W., Spalding, M. & Watkinson, A.R. (2012). A horizon scan of global conservation issues for 2012. *Trends in Ecology and Evolution* 27(1), 12-18.

- Svensson, S., Svensson, M. & Tjernberg, M. (1999). [*The Swedish Breeding Bird Atlas.*] Vår Fågelvärld, suppl. 31. Stockholm. (In Swedish)
- Tingley, M.W. & Beissinger, S.R. (2009). Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology & Evolution* 24(11), 625-633.
- Trombulak, S.C. & Frissell, C.A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, 14, 18-30.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters* 8: 857-874.
- van Horne, B. (1983). Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47(4), 893-901.
- Vepsäläinen, V., Pakkala, T., Piha, M. & Tiainen, J. (2007). The importance of breeding groups for territory occupancy in a declining population of a farmland passerine bird. *Annales Zoologici Fennici* 44(1), 8-19.
- Whittingham, M.J. & Evans, K.L. (2004). The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* 146, 210-220.
- Whittingham, M.J. (2007). Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *Journal of Applied Ecology* 44(1), 1-5.
- Whittingham, M.J. (2011). The future of agri-environment schemes: biodiversity gains and ecosystem service delivery? *Journal of Applied Ecology* 48(3), 509-513.
- Whittingham, M.J., Devereux, C.L., Evans, A.D. & Bradbury, R.B. (2006). Altering perceived predation risk and food availability: management prescriptions to benefit farmland birds on stubble fields. *Journal of Applied Ecology* 43(4), 640-650.
- Wilson, J.D., Whittingham, M.J. & Bradbury, R.B. (2005). The management of crop structure: a general approach to reversing the impacts of agricultural intensification on birds? *Ibis* 147: 453-463.
- Wolf, M. & Weissing, F.J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B-Biological Sciences* 365(1560), 3959-3968.
- Voříšek, P., Jiguet, F., van Strien, A., Škorpilová, J., Klvaňová, A. & Gregory, R.D. (2010). *Trends in abundance and biomass of widespread European farmland birds: how much have we lost?* <http://www.bou.org.uk/bouproc-net/lbf3/vorisek-et-al.pdf>.
- Xavier, P. (2008). *Switching costs and consumer behaviour: implications for telecommunications regulations*. Emerald Group Publishing Limited, Bingley, UK.
DOI: 10.1108/14636690810887517
- Ydenberg, R.C. & Dill, L.M. (1986). The economics of fleeing from predators. *Advances in the Study of Behaviour* 16: 229-249.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.H., (2009). *Mixed effects models and extensions in ecology with R*. Springer Science + Business Media, New York, USA.

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