

Latitudinal and altitudinal shifts in the
breeding distribution of an alpine passerine,
the Bluethroat (*Luscinia svecica svecica*), in
Norway during 1980-2014

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II

Abstract

Climate change drives species to shift their ranges towards the poles and towards higher altitudes. Arctic and alpine ecosystems are particularly vulnerable, as climate change happens faster in these regions than the global average. With this in mind, changes in the breeding distribution with regard to latitude and altitude of an alpine passerine, the Bluethroat (*Luscinia svecica svecica*), in Norway during 1980-2014 were investigated. Analysis was conducted using a site occupancy model with opportunistic citizen science data. Results show that the occupancy probability of Bluethroat in 1x1km areas declined substantially at lower and intermediate elevations and latitudes. The decline was especially severe in southern Norway and at lower elevations in northern Norway, while occupancy probability around optimal altitudes in northernmost parts of Norway remained fairly unaffected. These findings are congruent with the pattern of distribution shifts found for other alpine birds in Fennoscandia the last decades. There may be several proximate factors causing these shifts in breeding distribution, such as reduced food availability and increased competition.

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I dedicate this thesis to the memory of my late dog, Bretto, who loved birds just as much as I do, just in a slightly different way.

*Jon Valbjørn Hagelin
Blindern, June 1st 2015*

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1 Introduction

Understanding factors regulating the distribution of organisms forms the core of ecology (Brommer *et al.* 2012). As such, climate is a dominant factor (Pearson and Dawson 2003). Since 1750, human activity has led to an increase in atmospheric concentrations of the greenhouse gases carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O), leading to the contemporary anthropogenic climate change (IPCC 2013). The average global surface temperature, for ocean and land combined, has increased by 0.85 degrees Celsius in the period 1880-2012, and further warming is expected in the coming decades (IPCC 2013). In the current thesis changes in the distribution of Bluethroat (*Luscinia svecica svecica*) with regard to latitude and altitude was studied over more than three decades in Norway.

1.1 Climate change happens faster in Arctic and alpine areas than the global average

The rate of global warming is not equal in all parts of the world. Compared to lower latitudes the Arctic is warming up more rapidly than the global mean, a phenomenon termed polar amplification (Serreze and Francis 2006, IPCC 2013). Since 1875, the Northern hemisphere above 60°N latitude has warmed at a rate of 1.36°C per century, approximately twice as fast as the global average (Bekryaev *et al.* 2010). Mountain ranges such as the Alps (Beniston *et al.* 1997, Böhm *et al.* 2001) and the Rocky Mountains have also experienced temperature increases above the global average (Kohler and Maselli 2009). According to Gonzalez *et al.* (2010) the Arctic and alpine ecosystems are also the most vulnerable to climate change. The above average temperature increases in these regions have led to detectable changes in vegetation in the Arctic and alpine ecosystems the last decades. In the European Alps, alpine flora is responding to the milder climate by shifting towards higher altitudes (Pauli *et al.* 1996, Walther *et al.* 2005), and forest and shrubs are expanding into the Arctic tundra (Sturm *et al.* 2001, Lloyd *et al.* 2002, Wang and Overland 2004, Chapin *et al.* 2005).

Dramatic changes are predicted in these regions in the near future. The alpine treeline in the Swedish mountains, a part of the Fennoscandian mountain range, is projected to rise with several hundred meters over a 100-year timeframe, leading to a severe reduction and fragmentation of the treeless alpine heathlands (Moen *et al.* 2004); but see Van Bogaert *et al.* (2011). In combination with rising sea levels the encroaching vegetation is projected to shrink the area of the Arctic tundra to its lowest extent in at least the past 21,000 years, severely reducing the breeding area for many bird species and the grazing areas for land animals inhabiting the tundra biome (Hassol 2004).

1.2 Climate change and shifts in bird distributions

As a response to climate change species have been predicted to shift their ranges towards the poles (Davis and Zabinski 1992, Woodward 1992) and towards higher altitudes (Peters and Darling 1985). At the latitudes of Europe and North America it is now well documented that species distributions across a large number of taxa indeed are moving north and to higher elevations (Hickling *et al.* 2006, Chen *et al.* 2011). Changes seem to be proportionate with the degree of temperature increase, as shifts in species distributions have been largest in areas of the greatest warming (Chen *et al.* 2011). These trends are also documented in birds. Pearce-Higgins and Green (2014) conducted a meta-study showing that avian species distributions across mid- to high northern latitudes have in general consistently shifted northward with 0.76 ± 0.27 km per year, a mean shift of 15km over a 20-year period. The rate of distribution shifts may vary among different groups of bird species. In Finland, Brommer *et al.* (2012) found that the trend of northward range shifts was stronger for bird species predominately breeding in central Europe than for northern boreal and Arctic bird species.

In general, the rate of retraction of the southern range limits, driven by extinction, seems to be slower than the northward expansion, driven by colonisation (Thomas and Lennon 1999, Brommer *et al.* 2012, Pearce-Higgins and Green 2014). This may indicate that the latitudinal advances at the northern range limits actually happen faster than the retractions at the southern limits (Pearce-Higgins and Green 2014). Alternatively it may only appear so, due to failed detection of population declines, or a failure of attributing the decline to climate change at the southern limits of species ranges (Thomas *et al.* 2006). Concerning birds' ability to track climate change, Devictor *et al.* (2008) found that although birds are rapidly shifting their distribution northward, they are still lagging behind the northward change in temperature. They noted that this discrepancy may threaten the ability of birds to cope with climate change in the long run.

While there is strong evidence for *latitudinal* range shifts in birds, the evidence of upward shifts in *altitude* is less clear. Although some studies have found significant upward shifts in elevation in birds (Popy *et al.* 2010, Forero-Medina *et al.* 2011, Reif and Flousek 2012), it is noted by Pearce-Higgins and Green (2014) that most studies do not, and as many have found signs of species shifting to lower elevations. A possible explanation for the apparently weaker altitudinal than latitudinal response in range shift due to climate change may be that shifts in altitude is happening on a finer scale (tens of meters) compared to shifts in latitude (tens of kilometres). Hence, subtle shifts in altitude may be harder to detect than shifts in latitude (Pearce-Higgins and Green 2014).

1.3 Arctic and alpine bird species are particularly vulnerable to climate change

As global warming progresses, some species may escape the detrimental effects of global warming by retreating to higher latitudes and altitudes, but species already living in these regions may eventually find themselves with nowhere left to go, facing global extinction (Thomas *et al.* 2006). As a consequence of climate change in the Arctic, Virkkala *et al.* (2008) projected that more than 20 northern bird species inhabiting northern Fennoscandia will lose over 60% of their climatic space by year 2080. Worldwide, several hundred bird species are predicted to experience increased risk of extinction as a result of range contractions, due to the upward shift of their lower altitudinal limits, putting species already living at high altitudes at particular risk (Sekercioglu *et al.* 2008). Indications that bird species inhabiting alpine ecosystem are already affected by recent climate change were found by Lehikoinen *et al.* (2014) in the Fennoscandian mountain range. They found a substantial decline in abundance in 9 out of 14 alpine bird species in the period 2002-2012, concurrent with the warmest and wettest decade in forty years. The fact that long-distance migrants declined less than short-distance migrants and resident species suggests that the main reasons for the decline may be intrinsic to the mountain range (Lehikoinen *et al.* 2014), and not due to factors in the overwintering areas or along the migration routes.

1.4 Using citizen science data and a site occupancy model to investigate possible distributional changes of Bluethroat in Norway

The project objective was to investigate possible changes in the breeding distribution of an alpine bird species, the Bluethroat, in Norway the last 35 years (1980-2014). Changes in the breeding distribution with regard to latitude and altitude were emphasised to investigate whether Bluethroat showed a pattern of distribution change as expected due to climate change, and to compare it to what have been found for other bird species the last decades. A site occupancy model based on MacKenzie *et al.* (2002) was used, provided with observational data from the Norwegian citizen science database artsobservasjoner.no (Artsobservasjoner 2014). A site occupancy model estimates the probability of species occupancy in an area, and is based on species detection/non-detection data (Bailey and Adams 2005). Possible changes in the breeding distribution of Bluethroat using this approach would thus be detected as changes in occupancy probability.

Species are rarely detected with perfect accuracy. This may cause false absences to be recorded – incidences where investigators fail to detect a species that is actually present. If occupancy probability is estimated from detection/non-detection data

without accounting for the possibility of false absences, the estimates of occupancy probability will underestimate the true occupancy levels (Bailey and Adams 2005). The method developed by MacKenzie *et al.* (2002) enables the modelling of species occupancy probability when species detectability is less than 100%. Based on the pattern of species detection/non-detection from multiple surveys of the same sites during a season, estimates for the detection and occupancy probability parameters can be found.

Artsobservasjoner is an open access internet platform where members of the public can report personal species observations, and thus consist of so-called citizen science data (Devictor *et al.* 2010). Birds have proved a successful taxonomic group for citizen science as they are relatively easy to census for amateur naturalists and because they are attractive (Devictor *et al.* 2010). Further, birds are sensitive environmental indicators of environmental changes and ecosystem health (Sullivan *et al.* 2009), and are thus a species group well suited for studies on the impacts of climate change.

However, opportunistic citizen science data, as is the case with data reported to Artsobservasjoner, contain several kinds of biases that may potentially lead to artificial trends or mask existing trends (Van Strien *et al.* 2013). Firstly, surveyed sites are unevenly distributed in space, leading to geographical bias (e.g. Dennis and Thomas (2000)). Secondly, variable search efforts within sites due to the lack of standardization of observer effort may lead to observation bias. Lastly, reporting bias may arise when observers report only the species they find interesting. Van Strien *et al.* (2013) found that opportunistic butterfly and dragonfly data could be successfully used to draw inferences on distribution trends when analysed with occupancy models to avoid observation bias and other biases affecting detection. They deduced non-detections for a focal species from visits to a site where any species of butterfly or dragonfly were reported by an observer, while the focal species itself was not. However, by using reports of *any other* species than the focal species to obtain non-detection data they did not account for the possibility that a focal species may be observed, but not reported, because the observer found other observed species more interesting to report. This situation would lead to an apparent false absence, and increased heterogeneity in detection probability. In the current thesis I suggest an improvement to the method of Van Strien *et al.* (2013) of obtaining non-detection data by assigning the focal species a tailored group of non-target species that will reduce the risk of reporting-induced false absences, and thus reduce heterogeneity in detection probability.

The Bluethroat is a remarkably beautiful passerine bird that in Norway breeds primarily in the subalpine birch forests and low alpine heath lands in the Norwegian mountain range (Haftorn 1971, Thingstad 1994) (photo 1). It was chosen as a representative for alpine birds because of its popular status among hikers and amateur birders. Its conspicuous bright colours and its distinct song make it a bird most birders would consider worthy of registering.

Lehikoinen *et al.* (2014) provided updated knowledge on the population status of Bluethroat in Fennoscandia (Norway, Sweden and Finland) by measuring trends in

abundance between 2002 and 2012. While the trend was slightly positive in Finland, and slightly negative in Sweden, it was significantly negative in Norway. Importantly, the bulk of the sampling areas in Norway were primarily located in the south, while in Sweden and Finland the sampling areas were from inland locations at higher latitudes. Thus, the study by Lehtikoinen *et al.* (2014) indicates that the population of Bluethroat has been stable at high latitudes while it has declined at the latitudes of southern Norway. Their analysis was based on data from point counts along predetermined routes. The sites were situated in remote, sparsely populated areas far from roads, and the field work was conducted by paid surveyors (Lehtikoinen *et al.* 2014). By using data from volunteers through Artsobservasjoner the current thesis offers a low cost alternative to conventional data sampling across the whole of Norway. It also serves as a pilot project testing the utility of this citizen science database in scientific research and nature management, as this has so far not been conducted in Norway to the knowledge of the author.



Photo 1. Male Bluethroat (*Luscinia svecica svecica*). Photo by Bjørn Aksel Bjerke

2 Materials and Methods

2.1 Study area

In Norway the Bluethroat primarily inhabits the subalpine birch forests and the low alpine zone in the Norwegian parts of the Fennoscandian mountain range, but can in some places be found in other habitats (Thingstad 1994). Thus, data from all parts of the country were included to insure that no areas where Bluethroats occur were omitted.

The Fennoscandian mountain range stretches from 58°N to 71°N (Holten 1995). The large span in latitude from north to south leads to great variation in the light climate. During the growing season, the length of day varies from about 16h in the south to 24h in the north under a midnight sun. In the west, the mountains are characterized by steep and rugged slopes, incised by fjords and deep valleys. Further east, the central parts of the mountain range forms a plateau around 1000-1200 masl (Holten 1995). The highest peak is Galdhøpiggen (2469 masl). In the southern part of the mountain range the low alpine zone occurs at an altitude of 1100-1450 masl (Holten 1995) and at sea level in the far north (Lehikoinen *et al.* 2014). The low alpine zone is dominated by low vegetation such as grasses (*Gramineae*), dwarf birch (*Betula nana*), willows (*Salix* sp.) and Bilberry (*Vaccinium myrtillus*) (Holten 1995, Lehikoinen *et al.* 2014). The low alpine zone is gradually replaced by subalpine birch forest (*Betula pubescens* ssp. *czerepanovii*) at lower elevations. The subalpine birch forest forms a distinct zone covering a latitudinal range of about 50-300m (Lehikoinen *et al.* 2014). The subalpine birch forest is replaced by Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*) at even lower altitudes (Kullman and Öberg 2009).

2.2 Study species

The Bluethroat is a monogamous and territorial passerine (Krokene *et al.* 1996). The male's blue throat patch, with a rust-red central spot, makes it incredibly beautiful and impossible to confuse with other species. Matching its plumage, the males' song is remarkably beautiful, characterized by variation and improvisations. The female is visually less impressive and the throat patch is usually faint (Haftorn 1971).

In Norway the Bluethroat arrives at the breeding grounds in the second half of May. The males' song activity is initiated immediately after arrival and declines sharply towards the beginning of egg-laying. In northern Finland (69.5°N) (Merilä and Sorjonen 1994) and Sweden (65.5°N) (Arheimer 1982) the date of laying of the first egg was found to take place in the first half of June. Unpaired males, and males who fail breeding attempts, are known to continue singing later in the season, after the mated males have stopped. In addition to conventional singing, the male performs conspicuous song flights (Merilä and Sorjonen 1994).

The Bluethroat nests on the ground, laying 6-7 eggs. The eggs are incubated for two weeks, and the chicks fledge after another two weeks (Thingstad 1994). The diet consists of insects (Svensson *et al.* 2010). Both parents feed the chicks, but only the female incubates the eggs (Arheimer 1982). It migrates south to its wintering grounds in North-Eastern Africa to Western India during September (Svensson *et al.* 2010). The Bluethroat is predominately a Palearctic species, and occurs in several subspecies within its range. The nominate subspecies *L.s. svecica* breeds in Northern Fennoscandia through northern Russia and Siberia to north-west Alaska (Haftorn 1971). In Norway it occurs from the far south to the far north, where it primarily inhabits the sub alpine birch forests and the low alpine zone. In the latter habitat it is particularly associated with wetlands surrounded by lush vegetation of willow (*Salix spp.*) and dwarf birch (*Betula nana*) (Haftorn 1971, Thingstad 1994). In northern Norway the Bluethroat occurs at sea level, and on coastal islands in suitable locations with birch forest and willow (Haftorn 1971). It is also somewhat common in forest dominated by aspen (*Populus tremula*), Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Thingstad 1994). The total area covered by subalpine birch forest in Norway is approximately 30 000 km². In Thingstad (1994) it was estimated that the population size of Bluethroat in this habitat was in the order of about 200 000 pairs, with an average breeding density of about 6 pairs per km². The breeding density was found to be highest in the upper parts of these forests. Further, the low alpine area in Norway covers approximately 75 000-100 000km², and in this habitat the average breeding density of Bluethroat was found to be 5.5 pairs per km². Thus, the Bluethroat population size was estimated to consist of about 400 000-550 000 pairs in montane areas in 1994. Given that the Bluethroat is also somewhat common in other habitats as well, a crude estimate of the total population size for Norway was in 1994 approximately 500 000-1000 000 pairs (Thingstad 1994).

2.3 Acquisition of data

In order to promote a sound understanding of the origin and acquisition of data for this project, it is necessary to first introduce Artsdatabanken and two of its services dealing with species occurrences, namely Artsobservasjoner and Artskart. Artsdatabanken is a national database on biodiversity, subjected to the Norwegian Ministry of Education and Research (Artsdatabanken 2014). Artsdatabanken was established to enhance the knowledge of biodiversity, and has been operative since January 2005. Its main task is to convey updated and easily accessible information on species and ecosystems to the society (Artsdatabanken 2014).

Artsobservasjoner (2014) is a species report system developed by Artsdatabanken in cooperation with five member organisations of The Norwegian Biodiversity Network (SABIMA) (SABIMA 2014). It is dedicated solely to public registrations and encourages members of the public to report their own species observations in order to increase the report of species occurrence in Norway

(Artsobservasjoner 2014). Species observations are reported to Artsobservasjoner as so-called primary data, i.e. single observations of one or more individuals observed at a locality at a given time. A reported observation in Artsobservasjoner is also considered a report to the appropriate organisation within SABIMA dealing with the specific group of species, who is then responsible for assessing the validity of rare and usual observations. In the case of birds, Norsk Ornitologisk Forening (NOF) is the responsible organisation (Artsobservasjoner 2014). Registered observations are publically available (Artsdatabanken 2014).

All observational data on birds used in this project are derived from Artsobservasjoner, and thus only include data collected by volunteers. The volunteers are assumed to report opportunistic observations on their own initiative. The species observations submitted to Artsobservasjoner are also available in another database subjected to Artsdatabanken, called Artskart (Artskart 2014). Although data are available from the Artsobservasjoner website, data were acquired through Artskart due to the more efficient way of downloading large amount of data. In Artskart data from Artsobservasjoner are pooled together with data from other contributors, but reports stemming from Artsobservasjoner are labelled with "Artsobservasjoner" in the category "CollectionName". All reports are submitted with date of entry. Data for all species in this thesis were downloaded the 5th of December 2014.

2.4 Extraction of relevant data from Artsobservasjoner

The next step was to retain only the observations relevant for the project objective, which was to investigate changes in the *breeding distribution* of Bluethroat. Thus, for Bluethroat observations only those in the breeding season were of interest. Species observations in Artsobservasjoner are submitted with information on the following; date, number of individuals observed, age, gender, activity, observer comments, and locality with a measure of geographical uncertainty assessed by the observers themselves (Artsobservasjoner 2014). Observations of Bluethroat included in the analysis spanned from the 11th of May to the 23rd of August across all years. All observations within the 10th of June to the 15th of July were assumed to be of breeding individuals, and thus included in the data. I regard this time period to represent the core of the breeding season of Bluethroat in Norway and it is henceforth referred to as the "Prime season". Observations outside the Prime season were only included if they were submitted with an activity category clearly indicating breeding. The limits of the Prime Season may seem overly conservative, but are determined in order to safeguard the exclusion of non-breeding individuals. In spring, before the 10th of June, individuals may still be migrating and only moving through an area, and in late summer after the 15th of July individuals that have failed in breeding or fledged young may move into areas of breeding Bluethroat. These categories are as follows: "Nest, eggs/chicks", "Nest, chicks

heard”, “Failed breeding attempt”, “Incubating”, “Egg shell”, “Carrying feed to chicks”, “Carrying fecal sac”, “Visiting occupied nest”, “Pulli/newly fledged chick”, “Diversionary maneuver”, “Building nest”, “Incubation spot”, “Mating (or mating behavior)”, “Permanent territory”, “Pair in suitable habitat for breeding”, “Observation in breeding season, suitable breeding habitat” and “Nest in use”. Observations of non-target species included in the analysis were limited to the time span of included Bluethroat observations (May 11th – August 23rd). The limit of geographical uncertainty was set to $\leq 500\text{m}$ for observations of all species to reduce the risk of assigning observations to the wrong spatial unit (1x1km, see below). This criteria removed 317 (9%) of the Bluethroat observations within the Prime Season or with certain sign of breeding (3517 obs.). Artsobservasjoner allows observations made prior to its establishment in 2008 to be reported (Artsobservasjoner 2014), thus data are available several decades back in time. The period 1980-2014 was selected for this project as data for Bluethroat earlier than 1980 were considered too scarce to make strong inference.

2.5 Occupancy modelling when species detectability is imperfect

According to MacKenzie *et al.* (2006) ‘Occupancy is the natural state variable for use in studies of distribution and range’. A state variable is a variable that is used to quantify the status of a community or population. Occupancy is defined as the presence of at least one individual of a species in a defined area (MacKenzie *et al.* 2006). It is very common for animals and even entire species to go undetected during surveys. Thus, one can only make reliable inferences about occupancy probability if the imperfect detection of species is accounted for during data collection and analysis (MacKenzie *et al.* 2006). A model that accounted for this was first developed by MacKenzie *et al.* (2002), where the probability of species detection is estimated from multiple surveys of each site. A site is an area that acts as a sampling unit for species presence/absence, and can be naturally occurring spatial units, e.g. ponds or islands, or arbitrarily delimited areas of habitat. The basis of the conceptual model is that the outcome of whether a species is detected at a site is governed by two stochastic processes. First, a site i may be either occupied by the species (with probability Ψ_i) or unoccupied (with probability $1 - \Psi_i$). The model assumes that an occupied site remains occupied for the duration of the season (breeding season in this case). The second process is the detection of the species; if the site is occupied by the species, then at each survey j there is some probability p_{ij} of detecting it. Consequently, the probability of the species remaining undetected in the j th survey, given that the site is occupied by the species, is $1 - p_{ij}$. Obviously, if the site is unoccupied by the species, the detection probability is zero.

Ψ_i : the probability that a site i is occupied by a target species (occupancy probability).

p_{ij} : the probability of detecting the species at site i during the j th survey, given it is present (detection probability).

From multiple surveys, a detection history is formed for each site. For example, four detection/non-detection surveys at site i can be written as $h_i = [0,1,0,1]$. A verbal description of this detection history would be: “the site was occupied by the target species (because it was seen at least once), species was not detected during survey 1, species was detected during survey 2, species was not detected during survey 3, species was detected during survey 4”. However, equal sampling effort is not required across all sites, hence the number of surveys in each site may vary. Using the concepts of occupancy probability and detection probability, the probability of observing this particular detection history can be expressed mathematically as:

$$\Pr(h_i = [0,1,0,1]) = \Psi_i(1 - p_{i1})p_{i2}(1 - p_{i3})p_{i4} \quad (1.1)$$

where the parameter Ψ_i represents the phrase “site i was occupied by the target species” of the above verbal description of the detection history. Further, p_{ij} represents the phrase “species was detected in site i during survey j ”, and finally $(1 - p_{ij})$ represents the phrase “species was not detected in site i during survey j ”. It is assumed that the detection probability during each survey is independent of the outcome of the previous surveys in the site.

For sites where the target species is never detected, there are two possible explanations; either the species was present, but never detected, or the species was truly absent. The two alternative explanations are impossible to separate from the data, and hence both must be represented in the probability statement. For example, the probability of detection history $h_i = [0,0,0,0]$ would be represented mathematically as:

$$\Pr(h_i = [0,0,0,0]) = \Psi_i \prod_{j=1}^4 (1 - p_{ij}) + (1 - \Psi_i) \quad (1.2)$$

where $\Psi \prod_{j=1}^4 (1 - p_{ij})$ represents the situation in which the species is present, but not detected in any of the surveys, and $(1 - \Psi_i)$ represents the situation where the species is truly absent.

When a probability statement is made for all the s detection histories, the model likelihood for the observed data can be constructed as a product of the site-specific detection history probabilities:

$$L(\Psi, \mathbf{p} | h_1, h_2, \dots, h_s) = \prod_{i=1}^s \Pr(h_i) \quad (1.3)$$

The detection history at each site is assumed to be independent of the detection histories at other sites. The likelihood function in expression (1.3) can be used to estimate occupancy probability and detection probability using maximum likelihood techniques. The maximum likelihood estimates for detection- and occupancy probability in the current thesis was calculated using the function ‘occu’ in the software package ‘unmarked’ (version 0.10.6) (Fiske and Chandler 2011) in the statistical program R (R Core Team 2015).

Occupancy and detection probabilities are likely to vary with the characteristics of a site. By using a logit-link (log-odds) function the probability of occupancy and detectability of sites can be modeled as a function of measured covariates. The probability that a site i is occupied by a species, as a function of site covariates, can be expressed as a logit-linear function on the form:

$$\text{logit}(\Psi_i) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_N x_{iN} \quad (1.4)$$

Here, the occupancy probability of site i , on a logit scale, is a function of N covariates associated with the site ($x_{i1}, x_{i2}, \dots, x_{iN}$) and there are $N + 1$ coefficients (parameters) that are to be estimated: one intercept or constant term (β_0) and N regression coefficients for each covariate. The probability of occupancy can now vary across sites, but the parameter being estimated (the β s) are assumed to be constant across all sites. Thus, the types of covariates appropriate to model Ψ_i are those that remain constant for the duration of the season, such as habitat type, elevation and latitude.

For detectability there are two types of covariates that can be considered. The first type is those covariates that remain constant within a season, but vary among sites (indexed by i), as for occupancy probability. However, these covariates need not be the same as those used to model occupancy probability. The second type is those that may vary between surveys, such as local environmental conditions, day of year or surveyor experience. Hence, given species presence, the probability that the species is detected in site i during survey j , as a function of site covariates, can be expressed as:

$$\text{logit}(p_{ij}) = \beta_0 + \beta_1 x_{i1} + \dots + \beta_N x_{iN} + \beta_{N+1} y_{ij1} + \dots + \beta_{N+V} y_{ijv} \quad (1.5)$$

Here, x_{i1}, \dots, x_{iN} denote the N site-specific (season-constant) covariates associated with site i . y_{ij1}, \dots, y_{ijv} are the V site and survey-specific covariates associated with survey j of site i .

Model assumptions

Assumptions specific for single species-single season site occupancy models (MacKenzie *et al.* 2006):

- 1) The occupancy status at each site does not change over the survey season. In this case; if a Bluethroat is observed in a site during a survey, it is assumed that it will continue to occupy the site for the duration of the breeding season.
- 2) The probability of occupancy is constant across sites, or differences in occupancy probability are modeled using covariates.
- 3) The probability of detection is constant across all sites and surveys or is a function of site-survey covariates; there is no unmodeled heterogeneity in detection probabilities.
- 4) Detection of species and detection histories at each location are independent.

Assumptions specific for the current project:

- 5) Bluethroat is registered when observed.
- 6) Misidentification of species does not occur.

2.6 Converting observations from Artsobservasjoner into occupancy data

Detection/non-detection data are needed in order to utilize site-occupancy models to estimate detection and occupancy probability in an area. Obtaining non-detection data for a certain species, using opportunistic species registrations from a citizen science database such as Artsdatabanken, is not straight forward. Volunteers register only what they observe, providing detection-only data; they do not report species absence. Van Strien *et al.* (2010) and Van Strien *et al.* (2013) solved this problem by using the reported presence of other non-target species in a site to obtain non-detections for an unreported focal species in a particular survey. They did not, however, customize the list of such species to the species in focus, but used the presence of “any other” species belonging to the same species group (i.e. butterflies and dragonflies). I argue that the uncritical use of any other species than the focal species to obtain non-detections does not fully correct for observers tendency to report only the species they find interesting

(reporting bias). Using opportunistic citizen science data in occupancy modelling, false absences may arise in two different ways. Either the species is present in a site, but not detected, or the species is detected but not reported. The latter scenario may arise if the focal species is less popular than other species observed on the same occasion. To solve this problem I suggest that each focal species is assigned a customized group of carefully selected sympatric species that are considered less interesting to report than the focal species itself. Following this logic it is assumed that if an observer cares to report one of these less-interesting species, the focal species itself will also be reported *if* it is observed. By doing so the latter source of false absences will largely be avoided and much of the unexplained heterogeneity in detection probability between sites will be reduced. Species constituting the group of less-interesting species are henceforth termed background species.

For Bluethroat the following bird species were selected as background species based on their more or less sympatric distributions and their assumed lower popularity to observers compared to Bluethroat:

Brambling (*Fringilla montifringilla*)
Field fare (*Turdus pilaris*)
Hooded crow (*Corvus cornix*)
Meadow pipit (*Anthus pratensis*)
Mew gull (*Larus canus*)
Northern wheatear (*Oenanthe oenanthe*)
Raven (*Corvus corax*)
Redshank (*Tringa totanus*)
Redwing (*Turdus iliacus*)
Twite (*Carduelis flavirostris*)
Willow tit (*Poecile montanus*)
Willow warbler (*Phylloscopus trochilus*)

For the method to be consistent, not mixing detection-only and detection/non-detection data, a Bluethroat detection (1) was only included in the analysis if at least one background species was registered in the same site during the same survey. A Bluethroat non-detection (0) was recorded if any of the selected background species were recorded in a survey, while Bluethroat itself was not.

2.7 Modelling possible changes in the breeding distribution of Bluethroat

Type of site occupancy model used

There are several types of site occupancy models suitable to different scientific inquiries (MacKenzie *et al.* 2006). The type of site occupancy model utilized in the current thesis is a single-species single-season model, where the probability of detection- and occupancy probability were modelled as functions of covariates. The notation “single-season” may be confusing since the data covers breeding seasons from 35 years. However, in multi-season models the occupancy state (true occupancy or absence) in a site one year affects the occupancy probability in the site the next year. In contrast, in the single-season model used here the occupancy probability in sites from the same location, but in different years, are regarded as independent of each other.

Location and site construction

By using a UTM33 grid, the whole of Norway was divided into squares of 1x1km, henceforth referred to as locations. This was done by downloading terrain models of 50x50m resolution from (Kartverket 2014), that were then aggregated into 1x1km squares, matching the UTM33 grid. The aggregation procedure was conducted in the statistical program R, using the package “raster” (version 2.3.33) (Hijmans 2015). A location wherein at least one background species was registered in a particular year formed a site. Hence, a site is the synthesis between a specific location and a specific year; observations in the same location, but in different years, would thus belong to different sites. Values of site-specific covariates were then applied to these sites.

Covariates included in analysis:

Latitude (Site-specific)

The angle of the rays of the sun relative to the surface of the earth determines the amount of heat energy received, and thus latitude is the most important climatic factor (Dannevig and Harstveit 2014). The latitude for each site was given by the lower left corner of the respective location.

Altitude (Site-specific)

Temperature decreases with altitude by 0.5–1.0 °C/100m (Beniston 2003). Altitude is thus an important factor influencing the local climatic conditions, but its effect is

conditional upon the given latitude. Information on altitude was applied to each site from the terrain models downloaded from Kartverket (Kartverket 2014). Since the original resolution of these terrain models were 50x50 m, which were then aggregated into 1x1 km, the altitude in each location represents the arithmetic mean of the altitudes of the 50 x 50 m units comprising the respective location.

Year (Site-specific)

Year is included as a site-specific covariate, thus a characteristic of a given site.

Julian date (Survey-specific)

The survey date, expressed as Julian date, was included as a survey-specific covariate to investigate whether the detection probability varied with time of year.

Prime Season (Survey-specific)

As all categories of Bluethroat observations were included within the span of the Prime season (June 10th - July 15th), while observations outside this period only included observations with sure sign of breeding, the detection probability was assumed to be higher within the Prime season. This difference was thus accounted for by including Prime Season as an additive survey-specific covariate contingent on Julian date.

Modelling strategy

A priori assessments of how the given covariates would affect the detection- and occupancy probability of Bluethroat were done prior to modeling in order to reduce the number of candidate models to a manageable set that were biologically reasonable.

Akaike information criterion (AIC) was used as a means of ranking the predictive suitability of candidate models (Burnham and Anderson 2002). The method of AIC is based on the model likelihood, but encourages parsimony (i.e. models with as few parameters as necessary) by penalizing an increase in the number of parameters (MacKenzie *et al.* 2006). During model selection a suit of candidate models are compared and the model with the lowest AIC-value chosen as the best. The models need not be nested. The criterion is expressed mathematically as:

$$AIC = -2nll + 2k \quad (1.7)$$

Where nll is the negative log likelihood of a model, and k is the number of parameters in the model. The focus is on the absolute differences in AIC-value between models and not the AIC itself or relative differences. According to Burnham and Anderson (2002), as a rough rule of thumb, all models with an AIC-difference less than 2 to the AIC-value of the

model with the lowest AIC among the candidate models have substantial level of empirical support. The use of AIC does not guarantee that one ends up with a model that fits the data well, only that the model with the lowest AIC-value is expected to give the most correct predictions among the candidate models considered. Hence, a residual plot analysis was conducted in combination with AIC to assess how well the top-ranked model fitted the data (see Appendix, Fig. A3 and Fig. A4).

Modeling occupancy probability

The effect of latitude and altitude were included in all candidate models. It was assumed that the effect of latitude was logit-linear. The effect of altitude on occupancy probability was assumed to depend on latitude. Towards higher latitudes the treeline occurs at increasingly lower altitudes and the optimal altitude for the occurrence of Bluethroat is expected to follow this pattern. Thus, it only made sense to investigate the effect of altitude on occupancy probability in interaction with latitude. Further, it was anticipated that occupancy probability would increase with altitude up towards an optimum, presumed to be at the altitude of the sub alpine birch forest and low alpine heathland in a given area, and then more abruptly diminish as the low alpine zone bordered to the less vegetated zone above. Sign of such a relationship was discovered from the residual plots of preliminary models. A number of polynomial expressions (2-8 degrees) for altitude were assessed to find the best fit to this presumed relationship between altitude and occupancy probability. Starting values from the previous, lower-order models were used to optimize model fit during this assessment, and the model for detection probability was held constant (see Table 2 below). To investigate to what degree change in occupancy probability depended on latitude, the interaction between year and latitude was included in candidate models for occupancy probability.

Modeling detection probability

Bluethroat detection probability was assumed to be a function of Julian day, whether or not visits to locations were undertaken during the Prime Season, and altitude in interaction with latitude. It was anticipated that detection probability was likely to increase during spring as Bluethroats arrive, and decrease in late summer when they start to departure, thus a quadratic function of Julian date was used to model this seasonal pattern in detectability. In contrast to observations of Bluethroat within the Prime Season, wherein all observations of Bluethroat were included in the data, observations outside of this period had to meet strict criteria indicating breeding to be accepted. This meant that only a fraction of the observations outside the Prime Season would be included, leading to a lower detection probability. This difference in detection probability was accounted for by introducing the Prime Season covariate. It was further anticipated that detection probability would be higher on the treeless heathland in the low alpine zone than in the dense vegetation of the sub alpine birch forest at lower

altitudes because birds in open landscapes are easier to spot. Thus, in addition to Julian day and Prime Season, altitude (in interaction with latitude) was considered as a covariate indirectly affecting the detectability of Bluethroat.

3 Results

3.1 Overview of data

In total there were 66 313 unique location-year combinations (sites) with detection/non-detection data across all years. Of the 66 313 sites, Bluethroat was observed at least once in 1 768 (2.66%) of them. In each site there were conducted a varying number of surveys, ranging from 1 to 198 (mean 2.6, sd = 6.5) (Appendix, Table A1). A survey represents a visit to a site wherein at least one background species was observed along with the concomitant detection (1) or non-detection (0) of Bluethroat. While each survey is the result of the observations of a single observer, the different surveys in a site may stem from different observers. In total, 173 785 surveys were conducted across all sites, in which Bluethroat was observed in 2 209 (1.27%).

Across all years there were 27 039 unique locations (Fig. 1). As one location covers 1x1 km the total area covered in the research equals to 27 039 km², constituting 8.35% of the total area of the Norwegian mainland. Of the 27 039 locations, Bluethroat was seen at least once in 1 166 (4.3%) of them (Fig. 2). Most locations were visited only a few years (Appendix, Table A2).

Consistent with the increasing number of observations per year, the number of sites per year also increased with time, especially after the establishment of Artsobservasjoner (Appendix, Table A3). The proportion of sites in which Bluethroat was seen each year shows large annual fluctuations, but a strong negative trend with time (Fig. 3).

The number of observers contributing with observations, and the number of observations submitted each year, increased markedly with the establishment of Artsobservasjoner in year 2008. In total, 2 257 different observers contributed with observations to the thesis (Appendix, Fig. A1b).

In total, 431 215 observations of all species were obtained from Artsobservasjoner from the years 1980-2014, given the investigation criteria described in Materials & Methods (Table 1). The total number of Bluethroat observations within the PrimeSeason (10th June – 15th July), and the observations outside of this period with certain sign of breeding, was 3 517. Of these, 317 observations were omitted due to geographical uncertainty greater than 500m, leaving 3200 observations. The final step was to remove observations of Bluethroat that were not registered together with at least one background species in the same survey (site and date) by the same observer, in order to maintain observations as detection/non-detection data. This criterion removed 991 single observations of Bluethroat, leaving 2 209 observations that could be used in the site occupancy model. Thus, of the 3 517 Bluethroat observations within the Prime Season, or with sure sign of breeding, 62.8% met the method requirements.

**Table 1: Number of observations of all species included in the occupancy data.
N = 431 215**

Bluethroat	Twite	Brambling	Mew gull	Willow tit
2209	4926	13234	76930	9893
Field fare	Meadow pipit	Hooded crow	Willow warbler	Raven
42575	35751	52061	68969	17615
Redshank	Redwing	Northern wheatear		
48022	28512	30518		

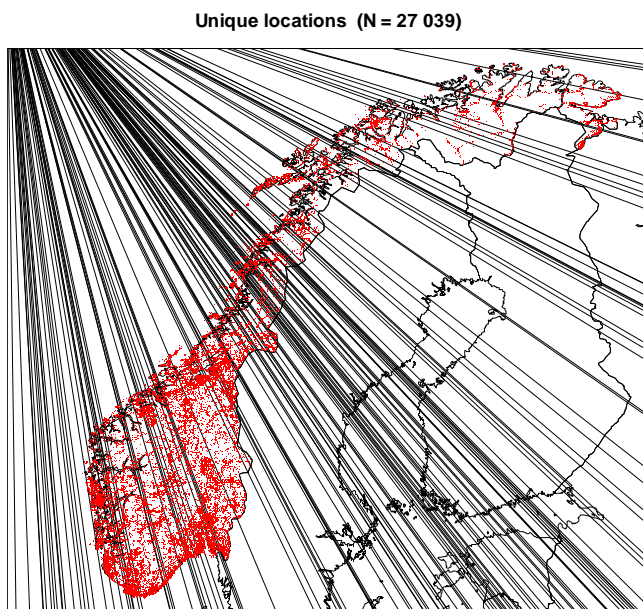


Figure 1. Unique locations with reported observations. Red points represent unique locations (1x1km) in which at least one observation of Bluethroat or its twelve background species were reported during 1980-2014. Locations are concentrated around areas of high human population density, with an overweight of locations in southern Norway. Points are not drawn to scale.

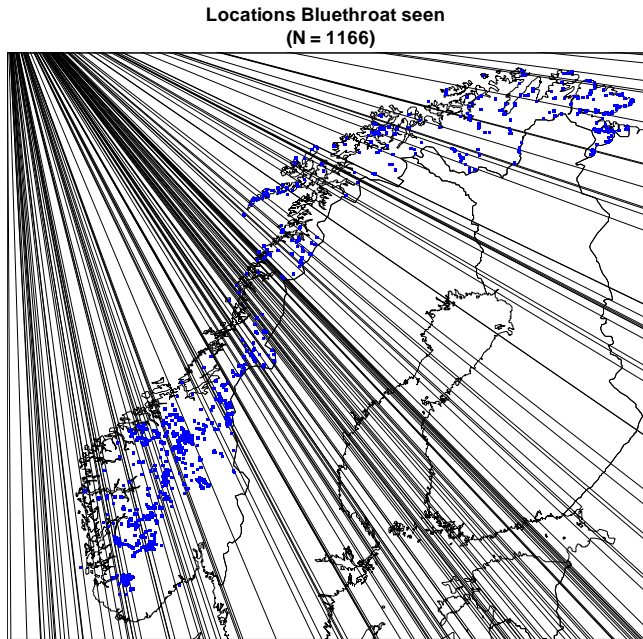


Figure 2. Locations (1x1km) in which Bluethroat was reported at least once during 1980-2014. Bluethroat was reported at least once in 1 166 locations, a fraction constituting 4.3% of the total number of locations. The points are enlarged for the purpose of visualisation.

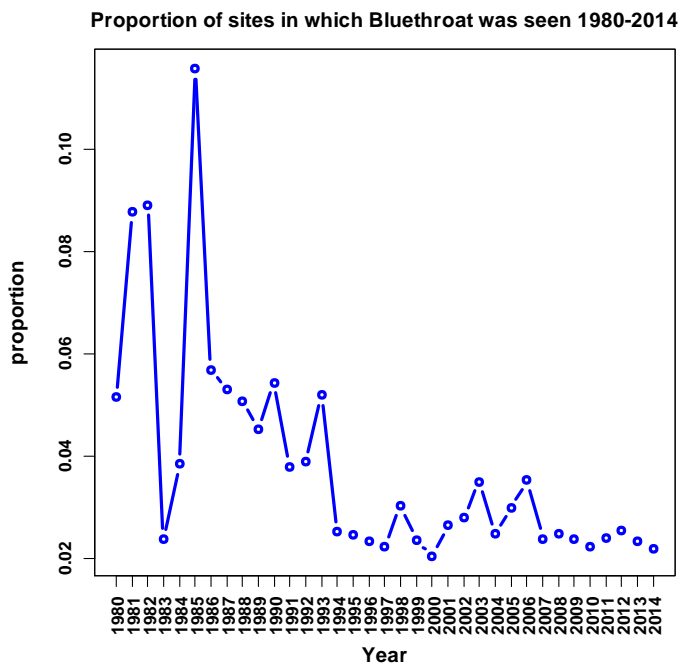


Figure 3. Proportion of sites in which Bluethroat was seen each year in the period 1980-2014. After large annual fluctuations in early years of the study period, the proportion of sites occupied by Bluethroat shows a strong negative trend towards 2014.

3.2 Model selection

The 5th degree polynomial expression for altitude gave the best model fit and the lowest AIC (Table 2, model F). A further reduction in AIC was obtained by including latitude in interaction with Julian day in the model for detection probability (p) (Table 2, model E). The rationale behind this choice was that it seemed reasonable that the detection probability with Julian day would vary across latitudes, as spring is later at northern latitudes, and birds arrive later. The detection probability model of model E was then added an interaction effect between altitude and latitude, which proved to give a considerable lower AIC-value (Table 2, model C). The interaction between latitude and Julian day in the detection probability model of model C was then tried removed, which resulted in a further reduction in AIC (Table 2, model B). This proved that the presumption that the latitude-Julian day interaction effect was not of great importance to detection probability. The occupancy probability model of model B was then added an interaction term between year and altitude (Table 2, model A). Although model A had a slightly higher AIC-value than model B, model A was chosen as the main model for inference due to its incorporation of a latitude-year interaction effect without considerable increase in AIC compared to model B.

A model with a three-way year-latitude-altitude interaction in the occupancy model was sought for in order to let the trends in occupancy probability over time vary with both altitude and latitude (Table 2, model D). This model was based on model B, but a version with a 4th degree polynomial expression for altitude, instead of the original 5th degree polynomial expression, proved to give a lower AIC-value. Although this model had a considerable higher AIC-value than model A-C, it was chosen for the task of revealing possible changes in occupancy probability with altitude over time.

More complex models for detection probability allowing detection probability to decline at higher altitudes (i.e., allowing bell-shaped curves) resulted in unstable model fits indicating that it is not possible to discern whether occupancy probability or detection probability is near zero at these altitudes, although model predictions at lower and intermediate altitudes changed little. This problem probably reflects the fact that there are fewer sites with replicated visits within seasons at high altitudes than at low altitudes. I therefore based my interpretation on the models that only included a logit-linear trend in detection probability with latitude, and note that model predictions for detection probability at high altitudes (where occupancy probability is predicted to be near zero) are unreliable.

Table 2: Assessed models for the detection- and occupancy probability of Bluethroat.

Model selection was based on AIC-values and an overall assessment of the model fit. date = Julian day; PS = Prime Season. Explanation of abbreviations for polynomial expressions of parameters: e.g. latitude*poly(date,2) means “latitude + date + date² + (latitude * date) + (latitude * date²)”

* The AIC-value of Model B is slightly lower than the AIC-value of Model A. Nonetheless, Model A has been chosen for inference due to its higher flexibility by the addition a year-latitude effect.

Model	Detection model (p)	Occupancy model (Ψ)	Parameters	ΔAIC
A	poly(date,2) + PS + (altitude * latitude)	latitude*poly(altitude, 5) + (year*latitude)	21	0.00
B	poly(date,2) + PS +(altitude * latitude)	latitude*poly(altitude, 5) + year	20	-0.11*
C	latitude*poly(date,2)+PS +(altitude*latitude)	latitude*poly(altitude,5)+year	22	4.54
D	poly(date,2) + PS + (altitude * latitude)	year*latitude*poly(altitude,4)	27	23.19
E	latitude*poly(date,2)+PS	latitude*poly(altitude,5)+year	20	25.23
F	poly(date,2)+PS	latitude*poly(altitude,5)+year	17	70.20
G	poly(date,2)+PS	latitude*poly(altitude,6)+year	19	74.20
H	poly(date,2)+PS	latitude*poly(altitude,7)+year	21	78.20
I	poly(date,2)+PS	latitude*poly(altitude,8)+year	22	82.20
J	poly(date,2)+PS	latitude*poly(altitude,3)+year	13	84.15
K	poly(date,2)+PS	latitude*poly(altitude,4)+year	15	88.15
L	poly(date,2)+PS	latitude*poly(altitude,2)+year	11	139.50

3.3 Model results

According to the predictions of model A, the occupancy probability of Bluethroat has undergone profound changes with latitude in Norway the previous 35 years. The pattern of change in occupancy probability can be seen for specific combinations of altitude and latitude in Fig. 5 (see also Appendix Fig. A4), and for the whole country in Fig. 6. To further investigate the pattern of change in occupancy probability, model predictions at four latitudes (59°N, 62°N, 66°N and 70°N) (Fig. 4) were chosen for comparison with respect to changes in occupancy probability with both altitude and latitude in four different years (1980, 1992, 2002, 2014). Through analysis of residual plots, model A was found to fit the data satisfactorily (Appendix, Fig. A2 and Fig. A3).

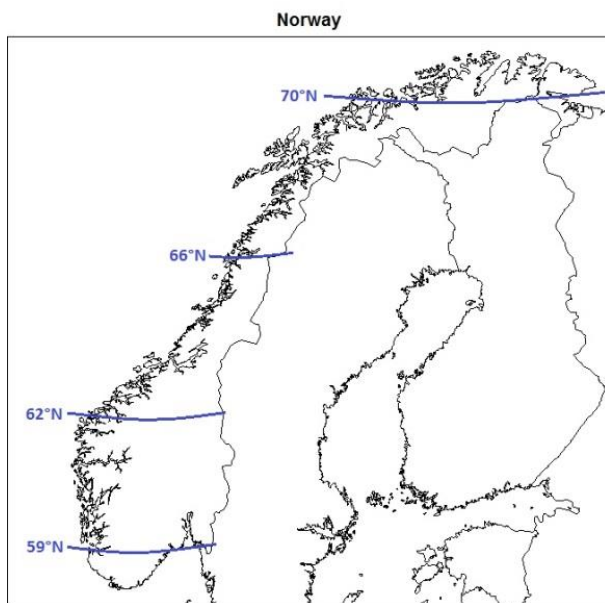


Figure 4. Map of Norway with lines showing the approximate position of the latitudes chosen for comparison of changes in occupancy probability with regard to latitude and altitude during the period 1980-2014.

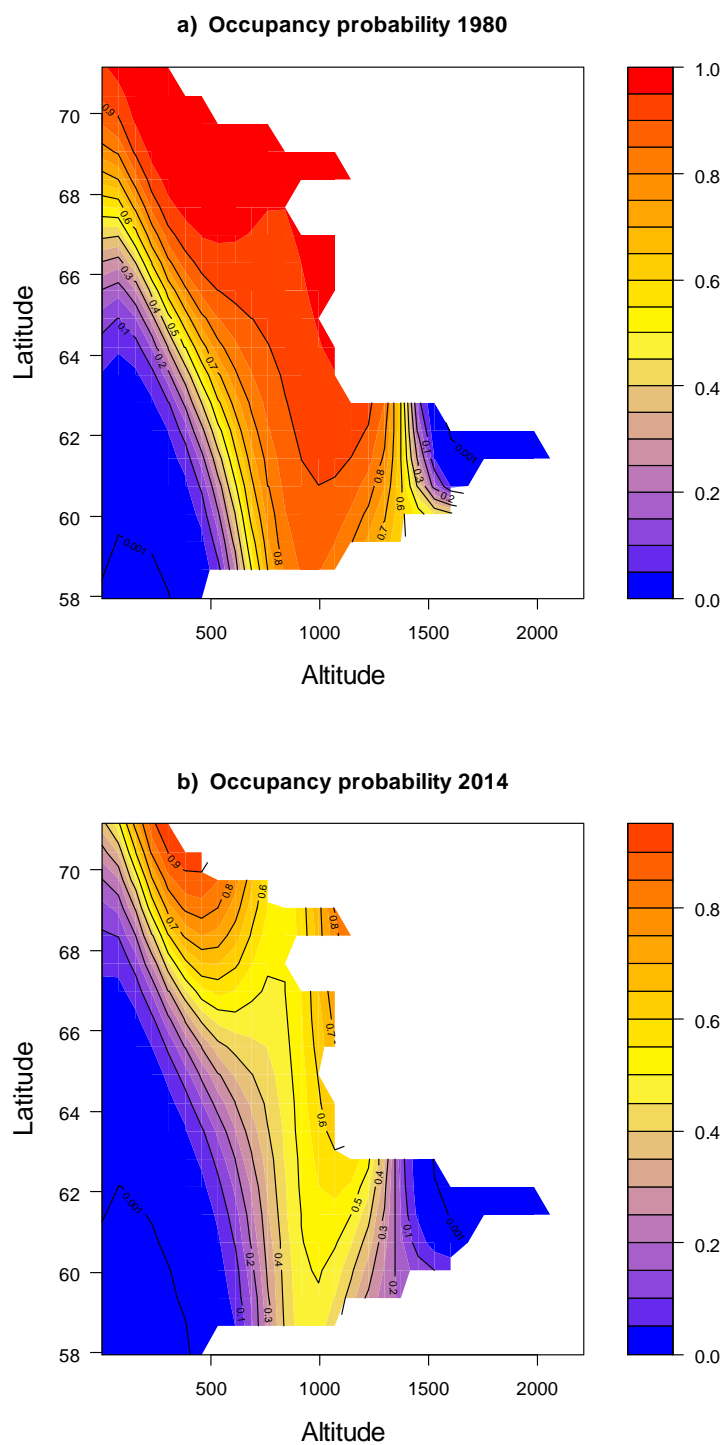


Figure 5. Model predictions of occupancy probability of Bluethroat as a combination of latitude and altitude (Model A). a) occupancy probability in 1980, b) occupancy probability 2014. While Occupancy probability was only weakly correlated with latitude in 1980 (a), there was a strong positive association between occupancy probability and latitude in 2014 (b). The blank areas in the two figures represent combinations of altitudes and latitudes for which there were no data.

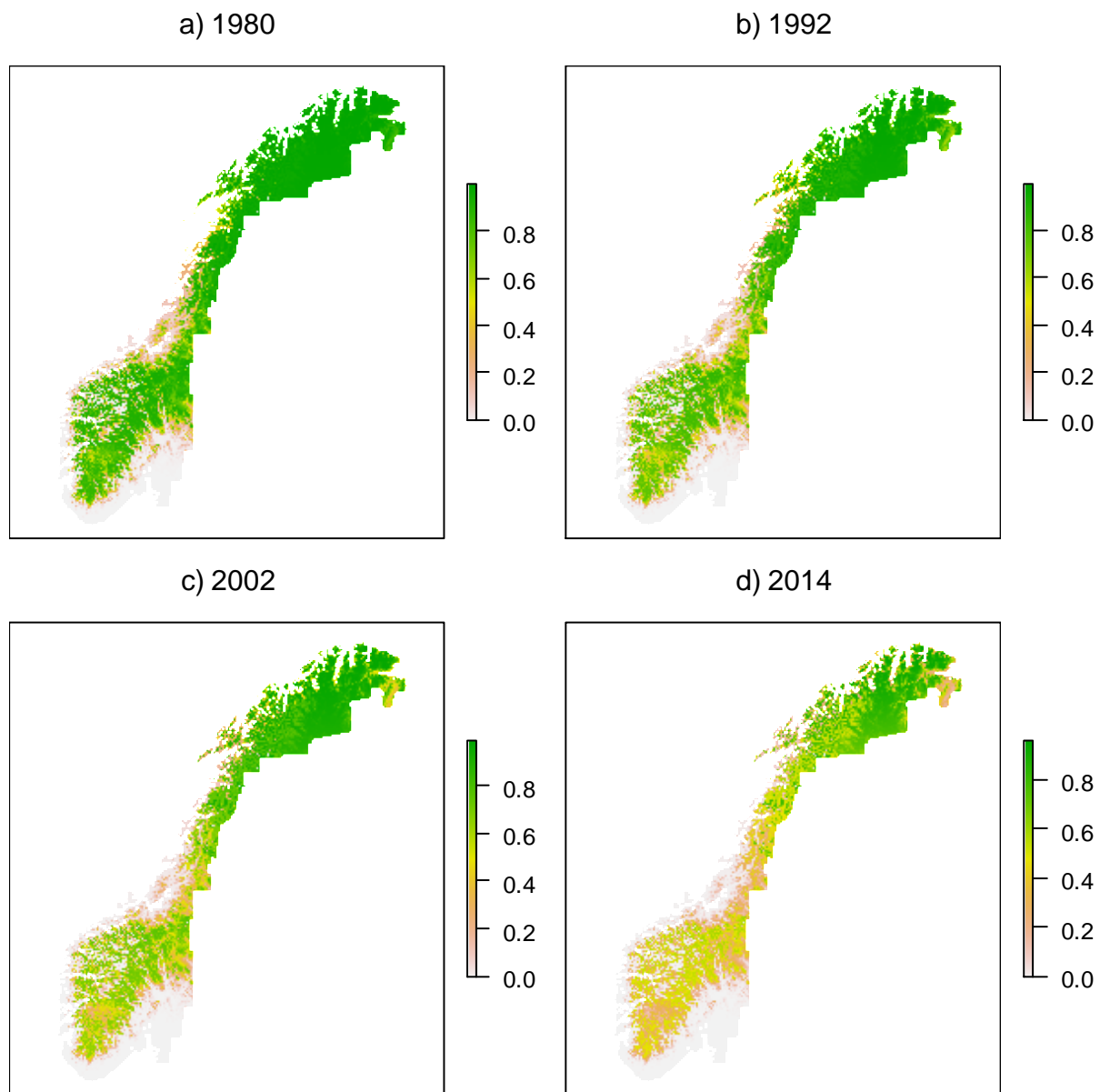


Figure 6. Model predictions of occupancy probability of Bluethroat projected on maps of Norway in four different years (Model A). a) 1980, b) 1992, c) 2002 and d) 2014. In this figure changes in occupancy probability of Bluethroat can be seen for the whole country. From being fairly high at all latitudes in 1980, occupancy probability of Bluethroat has gradually declined at the southernmost latitudes and northwards during the study period.

3.3.1 Patterns and changes in occupancy probability with respect to altitude

All results on changes in occupancy probability with respect to altitude were inferred from model D (Table 2), which allowed the logit-linear trends over years to depend on altitude and latitude. At the low to intermediate altitude range of the species distribution there were significant changes at all latitudes, with non-overlapping confidence intervals between predictions from 1980 and 2014 (Fig. 7). In the beginning of the study period (1980 predictions) the breeding distribution of Bluethroats at the two southern latitudes, 59°N (Fig. 7a) and 62°N (Fig. 7b), was confined to latitudes ranging from about 400-500 masl to about 1400-1500 masl. Within this range the occupancy probability was strongly bell-shaped with the highest occupancy probabilities concentrated within a quite narrow altitudinal range. At the same time at the northern latitudes, 66°N (Fig. 7c) and 77°N (Fig. 7d), occupancy probability was fairly high even down to sea level. This was especially pronounced at 70°N where there was only a slight difference in occupancy probability across the different altitudes (Fig. 7d). Data is lacking for the highest altitudes at the two northern latitudes, 66°N and 70°N, thus it is not possible to tell whether a similar bell-shaped pattern applied above the optimal altitude there, as for the two southern latitudes 59°N and 62°N.

Perhaps the most noteworthy change in occupancy probability as a function of altitude between 1980 and 2014 was the decline at lower altitudes at the northern latitudes 66°N and 70°N (Fig. 7c-d). According to model predictions, occupancy probability at sea level at 66°N was 0.22 (95% ci.: 0.07 to 0.49) in 1980 (Fig. 7c). In 2014, occupancy probability at sea level at this latitude was close to zero; 0.02 (95% ci.: 0.01 to 0.03), and the predicted occupancy probability of 1980 at sea level had risen to 422 masl. As for 70°N, the occupancy probability at sea level had declined from 0.81 (95% ci.: 0.50 to 0.95) in 1980 to 0.20 (95% ci.: 0.15 to 0.26) in 2014 (Fig. 7d). The predicted occupancy probability at sea level of 1980 at 70°N had risen to 567 masl in 2014. At 59°N in 1980 the altitude of occupancy probability 0.3 was 585 masl (Fig. 7a). In 2014 the altitude of 0.3 occupancy probability at 59°N had risen by 222 meters to 807 masl. At 62°N in 1980 there were two altitudes of occupancy probability 0.3; 461 masl (lower end) and 1287 masl (upper end) (Fig. 7b). In 2014 the lower-end altitude at 0.3 occupancy probability at 62°N had risen by 270 meters to 731 masl. The estimates of occupancy probability at higher altitudes than the optimum altitudes were generally too uncertain for meaningful inference about changes in the upper altitudinal range of the species. However, I note that occupancy probability at 62°N, where some high altitude data exist, changed little over the years (Fig. 7b).

Between 1980 and 2014 the altitude of maximum occupancy probability shifted upward at all latitudes, with the greatest shift at southern latitudes (Fig. 7a-d). Concomitantly, the maximum occupancy probability had declined at all altitudes and latitudes. At 59°N, the altitude of maximum occupancy probability in 1980 was 940 masl (occupancy probability: 0.94 (95% ci.: 0.57 to 0.95)) (Fig. 7a). In 2014, the altitude of

maximum occupancy probability had shifted 118 meters upward to 1058 masl (occupancy probability: 0.57 (95% ci.: 0.44 to 0.70)). At 62°N, the altitude of maximum occupancy probability in 1980 was 829 masl (occupancy probability: 0.93 (95% ci.: 0.84 to 0.97)) (Fig. 7b). In 2014, the altitude of maximum occupancy probability had shifted 204 meters upwards to 1033 masl (occupancy probability: 0.57 (95% ci.: 0.50 to 0.63)). At 66°N, the altitude of maximum occupancy probability in 1980 was 665 masl (occupancy probability: 0.97 (95% ci.: 0.80 to 0.98)) (Fig. 7c). In 2014, the altitude of maximum occupancy probability had shifted 263 meters upwards to 928 masl (occupancy probability: 0.6 (95% ci.: 0.40 to 0.75)). At 70°N, the altitude of maximum occupancy probability in 1980 was 511 masl (occupancy probability: 0.98 (95% ci.: 0.93 to 1.0(0.999)) (Fig. 7d). In 2014, the altitude of maximum occupancy probability had shifted 56 meters upwards to 567 masl (occupancy probability: 0.77 (95% ci.: 0.60 to 0.90)). Confidence intervals for the upward shift in altitude of the maximum occupancy probability have not been computed, and thus these estimates must be interpreted with caution.

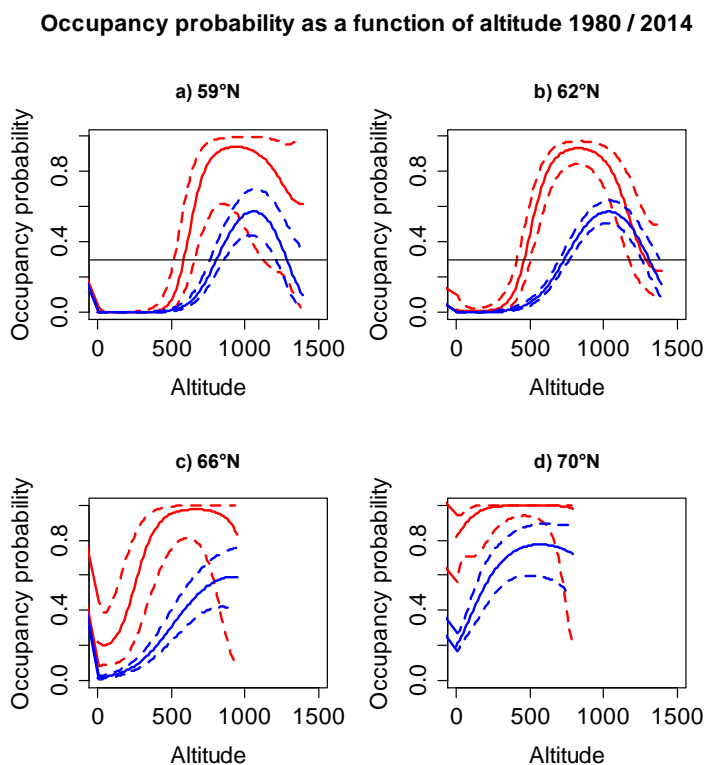


Figure 7. Occupancy probability of Bluethroat as a function of altitude at four different latitudes in 1980 (red) and 2014 (blue) (Model D). a) 59°N, b) 62°N, c) 66°N and d) 70°N. The horizontal line in a) and b) marks occupancy probability equal to 0.3.

3.3.2 Patterns and changes in occupancy probability with respect to latitude

During the course of the study period from 1980 to 2014 the occupancy probability of Bluethroat experienced a decline at optimal altitudes across all latitudes (Fig. 8a-d). The decline was, however, not evenly distributed. Most severe was the decline in occupancy probability in the south; at 59°N and the optimal altitude the occupancy probability went from 0.86 (95% ci.:0.73 to 0.94) in 1980 to 0.49 (95% ci.:0.39 to 0.60) in 2014 (43% decline) (Fig. 8a). The decline in occupancy probability at 62°N (Fig. 8b) and 66°N (Fig. 8c) showed a development very similar to each other. At 62°N, occupancy probability at the optimal altitude went from 0.92 (95% ci.: 0.87 to 0.95) in 1980 to 0.55 (95% ci.:0.50 to 0.62) in 2014 (40% decline). At 66°N, occupancy probability at the optimal altitude went from 0.95 (95% ci.:0.90 to 0.97) in 1980 to 0.56 (95% ci.: 0.40 to 0.71) in 2014 (41% decline). Least affected was the occupancy probability at 70°N (Fig. 8d); at the optimal altitude occupancy probability went from 0.99 (95% ci.: 0.984 to 0.998) in 1980 to 0.90 (95% ci.: 0.801 to 0.960) in 2014 (9% decline). At the end of the study period in 2014 there was a conspicuous positive association between occupancy probability of Bluethroat and latitude (Fig. 5b and Fig. 6d). For model predictions of occupancy probability of Bluethroat as a combination of latitudes and altitudes also in 1992 and 2002, see Appendix, Fig A4. Comparing model predictions for the whole country between different years during the study period (Fig. 6a-d), it is apparent that the occupancy probability initially declined at the southernmost latitudes and that the decline then steadily crept northwards.

Change in occupancy probability 1980-2014

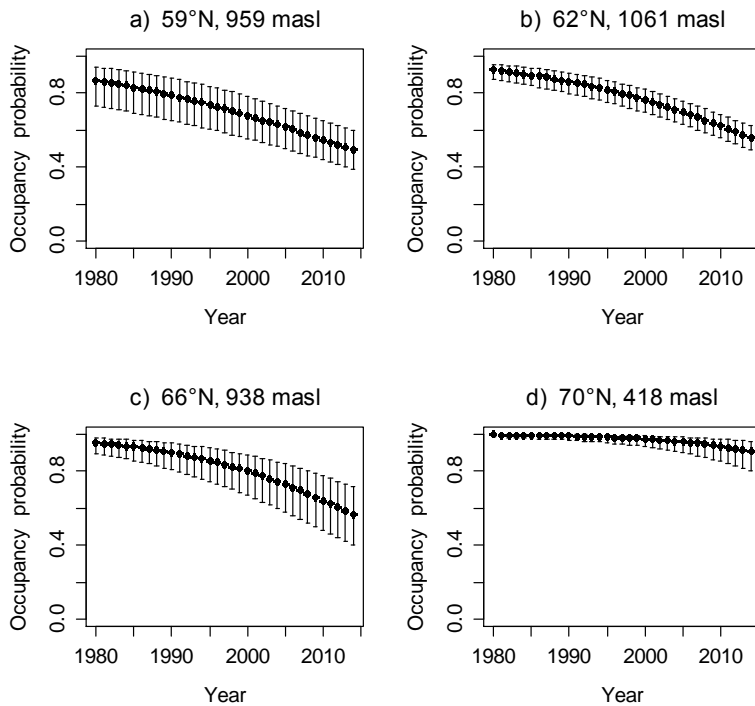


Figure 8. Changes in occupancy probability of Bluethroat from 1980 to 2014 at four different latitudes at the optimal altitude for each latitude (given above the plots). a) 59°N, b) 62°N, c) 66°N and d) 70°N. While occupancy probability declined at all four latitudes investigated during the study period, the decline was most severe at lower and intermediate latitudes.

3.3.3 Detection probability

Detection probability (model A) was estimated as a function of Julian day at optimal altitudes at the respective four latitudes 59°N, 62°N, 66°N and 70°N (Fig. 9). Maximum detection probability, over a breeding season, at optimal altitudes was highest at 59°N and 62°N with 0.39 (95% ci.: 0.34 to 0.45) and 0.39 (95% ci.: 0.36 to 0.42), respectively. At 66°N, the maximum detection probability estimate was 0.34 (95% ci.: 0.27 to 0.40), and at 70°N it was 0.24 (95% ci.: 0.20 to 0.29). The Julian day of maximum detection probability was day 180 (June 29th), assumed to be the same at all latitudes in this model. The Prime Season was of great importance to detection probability at all latitudes. The differences in detection probability across latitudes may reflect differing densities at the respective latitudes. Detection probability was also estimated as a function of altitude at different latitudes, as the detection probability model of Model A included an interaction between altitude and latitude for detection. Detection probability was weakly positively correlated with altitude at all latitudes (Fig. 10).

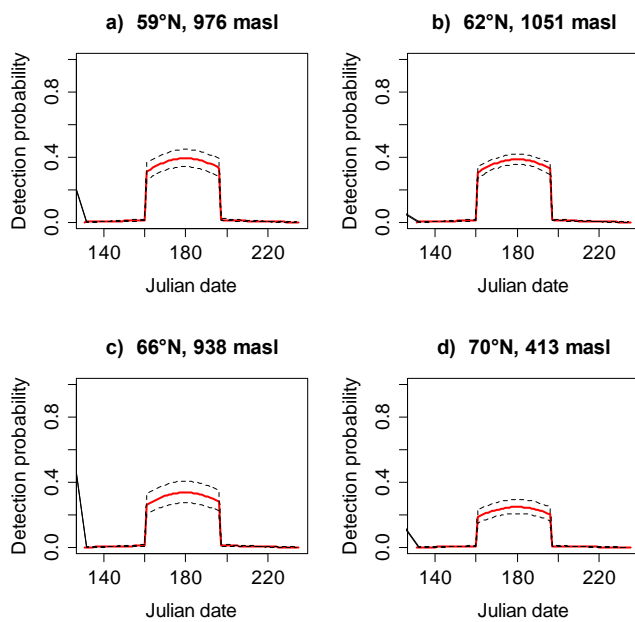


Figure 9. Estimated detection probability of Bluethroat as a function of Julian day at four different latitudes (model A). a) 59°N, b) 62°N, c) 66°N, d) 70°N. The given altitudes are the altitudes of maximum occupancy probability at the respective latitudes. Detection probability was highly influenced by the Prime Season (June 10th – July 15th), in which all observations of Bluethroat were interpreted as observations of breeding individuals. Maximum detection probability was highest at 59°N and 62°N, and declined successively at increasing latitudes.

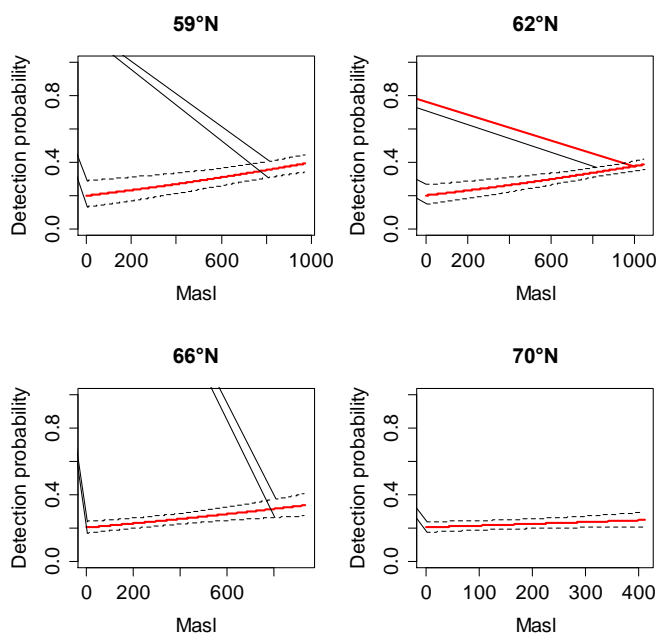


Figure 10. Detection probability of Bluethroat as a function of altitude at four different latitudes (Model A). a) 59°N, b) 62°N, c) 66°N and d) 70°N. Julian day = mean Julian day = 179 (28. juni) for all plots. While detection probability was positively correlated with altitude at all latitudes, the effect was weak in southern Norway and almost non-existent in northern Norway.

4 Discussion

Modelling the occupancy probability of Bluethroat in Norway 1980-2014, using opportunistic citizen science data from Artsobservasjoner, I found that occupancy probability has declined substantially at lower and intermediate altitudes and latitudes. These findings are concordant with what has been predicted as a response to a warmer climate (Peters and Darling 1985, Davis and Zabinski 1992, Woodward 1992) and with what have been found for other bird species during the last decades (Pearce-Higgins and Green 2014).

4.1 Changes in occupancy probability with altitude

According to the fitted model predictions, occupancy probability of Bluethroat has declined at low and intermediate altitudes, and the altitude of maximum occupancy probability has shifted upward for all latitudes investigated during the study period (Fig. 5).

Few studies have found significant altitudinal shifts in bird distribution in response to climate change. In the Italian Alps, Popy *et al.* (2010) investigated changes in mean elevation of birds between the periods 1992-1994 and 2003-2005 based on fine-scale (1x1km) atlas surveys with presence absence data. At the bird community level they found a significant overall shift in mean elevation of 29m towards higher altitudes, concomitant with a temperature increase of ca. 1°C in mean temperature between the two periods. However, they noted that the upward shift in altitude cannot unambiguously be interpreted as an effect of climate as other local factors might have influenced the pattern observed. At tropical latitudes, Forero-Medina *et al.* (2011) found an average upward shift of 49m for 55 species of birds in the Peruvian Andes in the 41 year period between 1969 and 2010. They used mist nests to sample bird communities at five different elevations between 690-2220 masl, and compared the weighted mean altitude between the two periods. Both Popy *et al.* (2010) and Forero-Medina *et al.* (2011) found that the altitudinal changes in bird distributions were smaller than expected from the changes in temperature. In the Italian Alps, Popy *et al.* (2010) found the response of the avifauna to be four to eight times lower than what was expected with the observed temperature increase. In addition, both Popy *et al.* (2010) and Forero-Medina *et al.* (2011) found that the trend of upward shift in distribution did not apply to all species investigated as the distribution of some species even shifted to a lower altitude.

Compared to the rather modest changes in altitudinal distribution found by Popy *et al.* (2010) in the Italian Alps and by Forero-Medina *et al.* (2011) in Peru, the findings in the current study are of a completely different order. This may be due to different relative warming at the respective latitudes leading to different rates of altitudinal shifts, or due to modelling artefacts and errors. Temperature data in Norway for the study

period was not included in the present study. However, in southern and northern Finland, temperatures increased by 1.4°C and 1.7°C between 1970 and 2012, respectively (Virkkala and Lehikoinen 2014). Southern Finland is at the same latitudes as southern Norway (about 60°N) and northern Finland borders to Finnmark, the northernmost county of Norway, at nearly 70°N. Despite a considerably higher rate of temperature increase at these northern latitudes compared to the Italian Alps the shifts in occupancy probability with altitude in Norway seems disproportionate, especially at 66°N and 70°N. This in particular considering the comparatively similar upward shifts of the avifauna across the huge difference in latitude between the Italian alps (Popy *et al.* 2010) and close to equator (Forero-Medina *et al.* 2011). In addition, the current results lack credible intervals, thus there exists no measure of the precision of change. The altitudinal changes in occupancy probability with altitude in Norway found in this study must therefore be interpreted with caution.

4.2 Changes in occupancy probability with latitude

According to model predictions, occupancy probability of Bluethroat in Norway has declined at all latitudes investigated, from 59°N to 70°N, during the study period. The largest relative decline in occupancy probability has taken place at southern latitudes. This pattern apparently indicates a retraction of the southernmost distribution of the species. It has, however, not been possible to detect any corresponding northward shift of the centre of optimal of occupancy probability as northern Norway from the beginning in 1980 already held this status.

These findings are congruent with the discoveries of Virkkala and Rajasärkkä (2011) in a study of population changes of bird species in Finland. They compared population changes of bird species in protected areas in the periods 1981-1999 and 2000-2009. They categorized species as either northern, southern, or distributed over the whole country. Bluethroat was included as a northern species. Using line transects to measure density, they found that populations of northern species had declined the most in southern protected areas. Concomitantly, they found that southern species increased most in northern protected areas, while populations of birds distributed over the whole of Finland showed a northward shift in density. Their findings also revealed that population declines of northern species were progressively severe towards the southern range boundary; the density of northern species declined with almost 50% in the southern protected areas, but only by 22% and 18% in central and northernmost protected areas of Finland, respectively. The increasing decline at the southern distribution boundary for northern bird species matches the pattern of change in occupancy probability of Bluethroat in Norway found in the present study. However, changes in abundance may take place without affecting occupancy probability. Importantly, their findings indicate that the pattern of decline at the southern distribution margin is not unique for Bluethroat, but applies to many other bird species with a northern distribution in Fennoscandia. Further evidence for a northward

distribution shift of both southern and northern birds in Finland was found by Brommer *et al.* (2012). They compared changes in the weighted mean latitude of species' distribution, using the results from three atlas surveys conducted between 1974 and 2010 using presence/absence data. According to their results the rate of retraction at the southern distribution margin for northern birds seemed to happen at half the rate of the northward expansion of southern birds. However, they note that their method lacked a standard measure of survey effort and that they therefore cannot critically assess to what extent changes in effort and changes in true occupancy are responsible for the pattern observed.

The current findings also provided a more detailed picture of the population status of Bluethroat in Norway than did the results of Lehtikainen *et al.* (2014). They found a significant decline in abundance for Bluethroat in Norway as a whole, but this was based on a limited number of sites mainly located in southern parts of the country. The current findings are congruent with a decline in southern Norway, but indicate a situation in northern Norway more similar to what was found for Sweden and Finland, where the populations have been quite stable. While the current study had far more sites than Lehtikainen *et al.* (2014) (66 313 vs 135 in Norway, respectively), the sites in the current study were not randomly selected. Thus, the sites of Lehtikainen *et al.* (2014) may have been more representative for the specific areas surveyed. Importantly, the results of Virkkala and Rajasärkkä (2011) and Lehtikainen *et al.* (2014) were based on abundance and density data, while the present study used presence/absence data. Brommer *et al.* (2012) also used presence/absence data, but did not adjust for detection probability and effort.

4.3 Possible proximate causes of decline in occupancy probability of Bluethroat due to climate change at low altitudes and latitudes

As the pattern of decline in occupancy probability of Bluethroat in Norway the last decades are concurrent with what is expected as a response to climate change, it is of interest to look at possible proximate causes driving the observed pattern. Few studies on climate change-induced species range shifts have identified the proximate factors driving the change. In those who have, changes in species interactions have been identified as the cause, especially those that lead to decreases in food availability and disease, rather than temperatures exceeding species' physiological tolerance (Cahill *et al.* 2013). There are examples of such biotic proximate factors affecting bird populations. Benning *et al.* (2002) found that endemic birds on the Hawaiian Islands are losing their malaria free refuges at high elevations as climate change enables the malaria parasite to infect birds at increasingly higher elevations. Pearce-Higgins *et al.* (2010) found that changes in the golden plover population were negatively correlated with high August temperatures in England. High August temperatures lead to desiccation and low survival

of instars of cold-adapted crane flies (Tupilidae), on which the golden plover (*Pluvialis apricaria*) heavily depends. They predict that the direct negative effect of climate change on crane fly abundance may lead to northward range contraction of the golden plover if warming continues.

For insectivorous birds it is important that they time their breeding so that it coincides with the peak abundance of insect prey in spring (Lack 1968). Adaptation to climate change by long-distance migrants may be constrained by inflexibility in their timing of spring migration. While climate change advances the spring phenology on their breeding grounds, the timing of migration of some species may be governed by endogenous factors, such as day length, that is not affected by climate change (Both and Visser 2001). Møller *et al.* (2008) found that, between 1990 and 2000, populations of European migratory bird species that showed the least response in their timing of breeding to advancing spring phenology declined, whereas species that were able to advance their timing of migration in step with climate change did not. Karlsen *et al.* (2009) compared the onset of the growing season in Norway between 1982 and 2006. They found that the onset of the growing season in Norway had advanced by 1-2 weeks in coastal and lowland areas of southern Norway, while in northern Norway the onset of the growing season remained the same, or even occurred later. If the Bluethroat has been unable to respond to this change by advancing its timing of migration, a mismatch between timing of arrival and the peak of insect prey might have been a proximate factor causing the observed decline in occupancy probability at low latitudes and altitudes in Norway. However, Lehikoinen *et al.* (2014) found that both alpine migrant and resident bird species declined, indicating a more complex pattern. The lesson from Pearce-Higgins *et al.* (2010) underlines the importance of having sound knowledge on which species a focal species depends, and how climate change affects them, in order to find the proximate causes of climate change-induced decline. Thus, the key to finding the proximate causes of decline of Bluethroat in Norway may be to improve the understanding of how climate change affects its most important prey species.

Further, as climate change facilitates northward range expansion of bird species originally having a more southern distribution (Virkkala and Rajasärkkä 2011, Brommer *et al.* 2012), previously allopatric species may become sympatric, or the abundance of southern species may increase at higher latitudes and altitudes. This may lead to new competitive species interactions, or intensify existing ones, respectively. Moreover, abiotic conditions are known to influence the outcome of inter-specific competition (e.g. Montchamp-Moreau (1983), Warner *et al.* (1993) and Wethey (2002)). Hence, another possible proximate cause of the observed decline of Bluethroat at low latitudes and altitudes may be due to new adverse interactions with invading species that benefit from a milder climate, or due to shifts in the competitive balance between Bluethroat and existing competitors to the disadvantage of the former.

Lastly, although the trends in occupancy probability of Bluethroat show a pattern as expected in response to climate change, one must be careful in attributing these trends solely to this factor. Speed *et al.* (2010) experimentally proved that herbivores

can limit the tree line to below its potential. As the use of upland areas as summer pastures for livestock have ceased in many areas the past century, the current encroachment of forest into previously open heathland may not stem from climate change alone, but be part of natural succession as herbivore pressure has been reduced (Penniston and Lundberg 2014). The conversion of open heathland areas into forest the last decades may have influenced the performance of Bluethroat either directly or indirectly, possibly contributing to the observed changes in occupancy probability.

4.4 Methods

The more potential background species a focal species has the more data is likely to be available in terms of sites and surveys. Thus, the method may not be well suited for less popular species, as they would have fewer potential background species. For Bluethroat, however, there were only minor discrepancies between data and the fitted model in residual plots (model A), showing a good model fit.

Probably reflecting differences in human population density, locations were more numerous in southern than in northern Norway (Fig. 1). Locations were concentrated around areas of high human population density and activity; from Fig. 1, cities and popular hiking areas such as the Lofoten archipelago can be identified as dense aggregations of locations. Still, the country as a whole was fairly well sampled as there were few large contiguous areas completely void of locations. There is a sharp division in the amount of data before and after the establishment of Artsobservasjoner in 2008 (Appendix, Fig A1a). Prior to its establishment the amount of data was sparse. Understandably, few people probably kept record of observations when no platform existed to publish them. In the year of establishment of Artsobservasjoner the number of observers and observations rose abruptly, and continued to rise in all subsequent years. Estimates of detection and occupancy probability are thus more reliable in the years succeeding the establishment of Artsobservasjoner than the preceding years, due to more data.

Many ecological processes occur at geographic scales beyond the reach of ordinary research methods (Dickinson *et al.* 2010). Thus, citizen science, being particularly useful to address issues spanning large temporal and spatial extents (Devictor *et al.* 2010), may be the only practical solution to achieve the geographic reach required to document ecological processes and address ecological questions such as species range shifts, broad-scale population trends and impacts of climate change (Dickinson *et al.* 2010). Hence, the use of citizen science data from Artsobservasjoner in combination with occupancy models could therefore be a powerful tool for conservation and nature management. Occupancy models have previously been found to perform well in interpreting citizen science data. Van Strien *et al.* (2013) found that trends in opportunistic data on butterflies and dragonflies, found with occupancy models, were well-matched with trends found in monitoring data. They further claim that there is

little evidence that other methods than occupancy models are capable of coping with reporting and detection bias in opportunistic citizen science data.

4.5 Conclusion

Using an occupancy model, with opportunistic citizen science data, substantial declines in occupancy probability of Bluethroat has been detected at lower altitudes and at southern latitudes in Norway the last 35 years. The pattern observed is consistent with distribution changes predicted as a response to climate change, and what has been found for other species of birds the last decades.

From the current results there is evidence for significant decline in occupancy probability below optimal altitudes, suggesting a range contraction happening at the lower distribution limit. The uncertainty of model predictions above optimal altitudes is too large to detect any concurrent range expansion of the upper distribution limit. The estimates of upward shift in occupancy probability of Bluethroat found in this study stand apart from the results in other studies by being of a much greater magnitude. However, these estimates lack measures of uncertainty, and must therefore be regarded as general trends rather than exact results.

The decline in occupancy probability with latitude began at the southernmost latitudes and steadily crept northward during the study period; only in the far north have the occupancy probability of Bluethroat remained reasonably unchanged. Most severe decline in occupancy probability happened at the southernmost latitude investigated.

Several biotic proximate factors may have caused the observed pattern. First, climate change may have affected the species on which the Bluethroat depends, changing the timing or amount of available food during the breeding season. Second, with the warmer climate new competitors may have arrived, or the balance of existing inter-specific competitive interactions may have changed in disfavour of the Bluethroat. A third possible factor contributing to the decline, not connected to climate change, may stem from the discontinuation of livestock grazing leading to forestation of previously open heathland. Of course, several proximate factors may act in concert. To enhance the understanding of how climate change affects the distribution of Bluethroat in Norway, further study should focus on identifying which species are the most important to Bluethroat, and on understanding how climate change affects them and their interactions with Bluethroat.

The current study shows that occupancy models can be successfully utilised to discover trends in distribution of a species using opportunistic citizen science data. It further demonstrates the benefit of public involvement in collecting biological data, and the great resource Artsobservasjoner can be for research and nature management.

5 References

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6 Appendix

Table A1: Number of sites and surveys per year			
Year	Sites	Surveys	Surveys per Site
1980	233	512	2.2
1981	285	675	2.4
1982	303	698	2.3
1983	294	820	2.8
1984	312	799	2.6
1985	363	780	2.1
1986	281	677	2.4
1987	396	937	2.4
1988	355	722	2.0
1989	419	871	2.1
1990	405	849	2.1
1991	553	1060	1.9
1992	463	891	1.9
1993	539	1106	2.1
1994	555	1129	2.0
1995	691	1400	2.0
1996	600	1244	2.1
1997	536	1160	2.2
1998	462	1013	2.2
1999	591	1357	2.3
2000	685	1634	2.4
2001	716	1517	2.1
2002	783	1789	2.3
2003	970	2190	2.3
2004	1045	2224	2.1
2005	1069	2194	2.1
2006	1162	2499	2.2
2007	1509	3236	2.1
2008	3546	8098	2.3
2009	6015	15800	2.6
2010	7437	20312	2.7
2011	7183	20068	2.8
2012	7704	22191	2.9
2013	8559	24882	2.9
2014	9294	26451	2.8
SUM	66313	173785	2.6

Table A2: Number of locations visited the given number of years				
1 year	2 years	3 years	4 years	5 years
14675	4862	2441	1521	1083
6 years	7 years	8 years	9 years	10 years
733	473	286	236	130
11 years	12 years	13 years	14 years	15 years
112	75	76	41	53
16 years	17 years	18 years	19 years	20 years
50	18	31	21	16
21 years	22 years	23 years	24 years	25 years
16	7	15	7	7
26 years	27 years	28 years	29 years	30 years
6	4	5	10	8
31 years	32 years	33 years	34 years	35 years
7	2	5	4	3

Table A3: Number of sites pr. year						
1980	1981	1982	1983	1984	1985	1986
233	285	303	294	312	363	281
1987	1988	1989	1990	1991	1992	1993
396	355	419	405	553	463	539
1994	1995	1996	1997	1998	1999	2000
555	691	600	536	462	591	685
2001	2002	2003	2004	2005	2006	2007
716	783	970	1045	1069	1162	1509
2008	2009	2010	2011	2012	2013	2014
3546	6015	7437	7183	7704	8559	9294

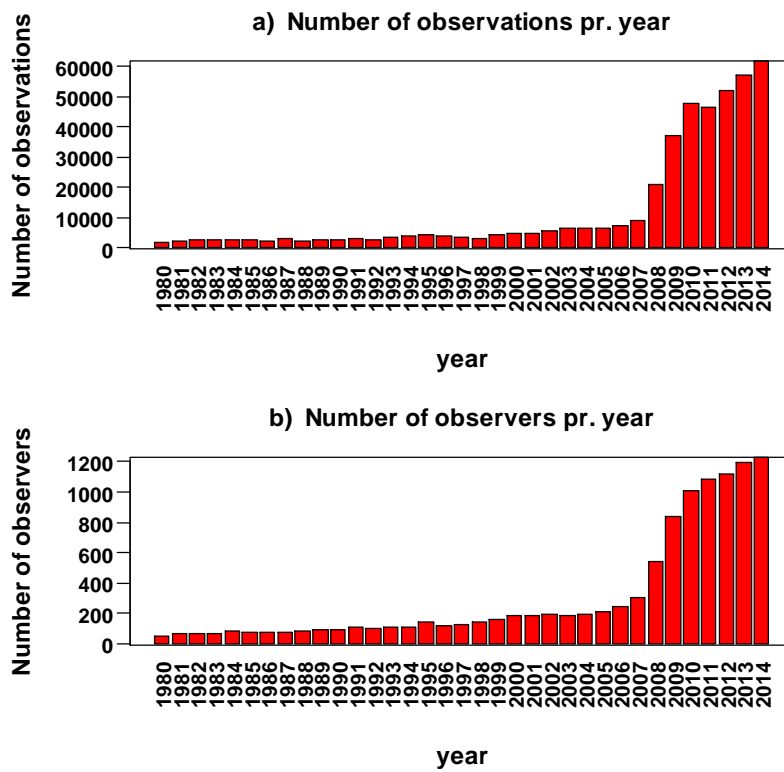


Figure A1. Overview of the annual number of observations and observers contributing with data to the thesis through Artsdatabanken. a) The number of observers contributing with observations each year of the study period (1980-2014). b) The number of observations submitted by all observers in the same period. Both the number of observers and the number of observations submitted showed a significant increase in 2008, the year of establishment of Artsobservasjoner, and continued to increase in the subsequent years.

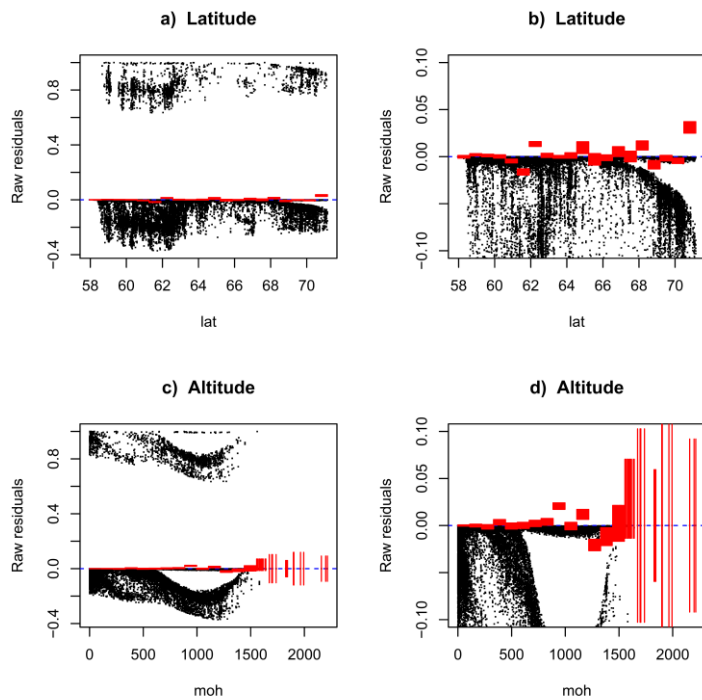


Figure A2. Residualplot of latitude and altitude for Model A. a) residualplot of latitude, b) residualplot of latitude zoomed in, c) residualplot of altitude, d) residualplot of altitude zoomed in. Units represent the average of residuals within discrete intervals of latitude or altitude, respectively. For latitude each unit represent the average of residuals within 0.66 latitudes. For altitude each unit represent the average of residuals within 111 meters. The height of the units represents the 95% confidence interval. In cases where the 95% confidence intervals do not overlap with zero, the discrepancy between model predictions and data are significant. For latitude (a-b), there are only small and unsystematic discrepancies between predicted values and data, signifying a good model fit. For altitude (c-d) there is a reasonably good fit between predictions and data, with slight underestimation of predicted values around 1000 masl. Above about 1500 masl confidence intervals widens, signifying less data and thus higher uncertainty in how well model predictions are congruent with data.

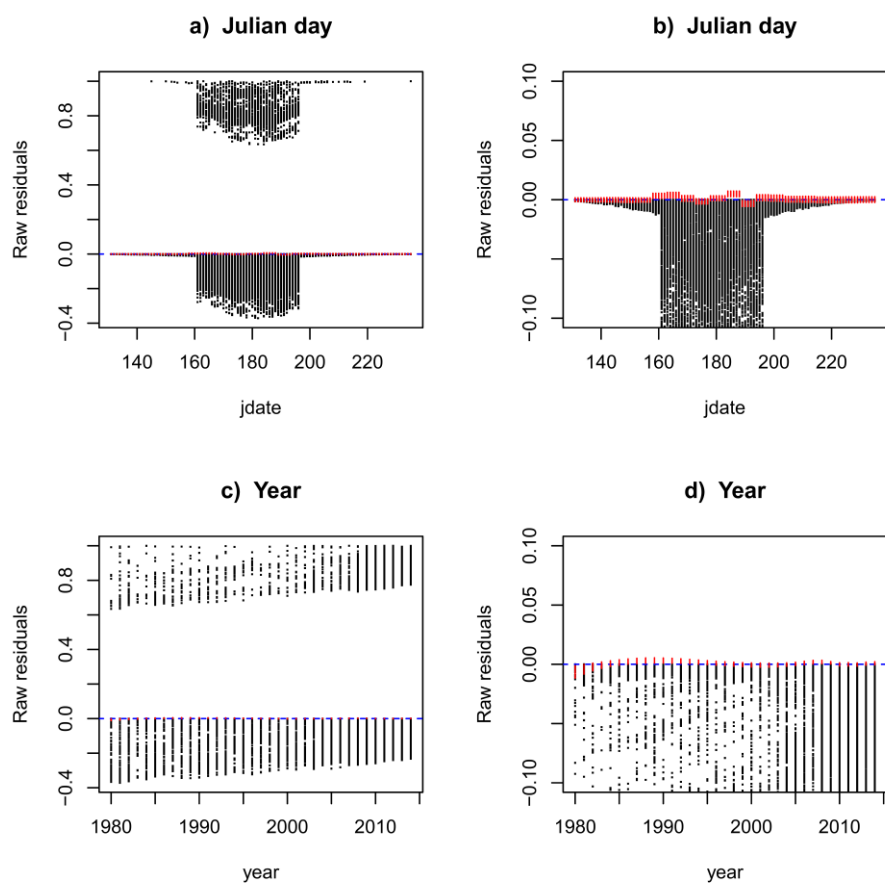


Figure A3. Residual plot of Julian day and year for Model A. a) Julian day, b) Julian day zoomed in, c) year, d) year zoomed in. For Julian day (a-b) units represent the average of residuals within intervals of 5.2 days. In c-d, residuals are plotted for each year between 1980 and 2014. The height of the units represents the 95% confidence interval. In cases where the 95% confidence intervals do not overlap with zero, the discrepancy between model predictions and data are significant. Although there are significant discrepancies between predicted values for Julian day and data, these are small (a-b). For year (c-d) there were no significant discrepancies between model predictions and data.

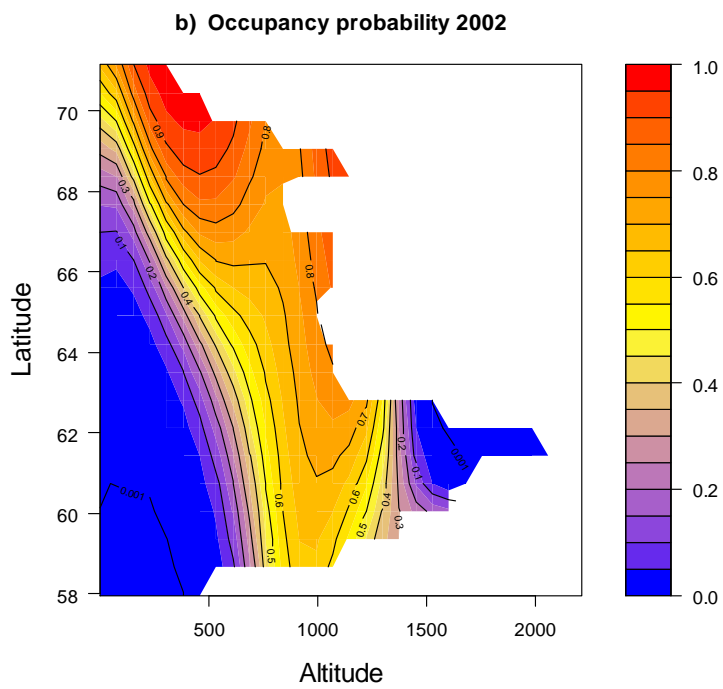
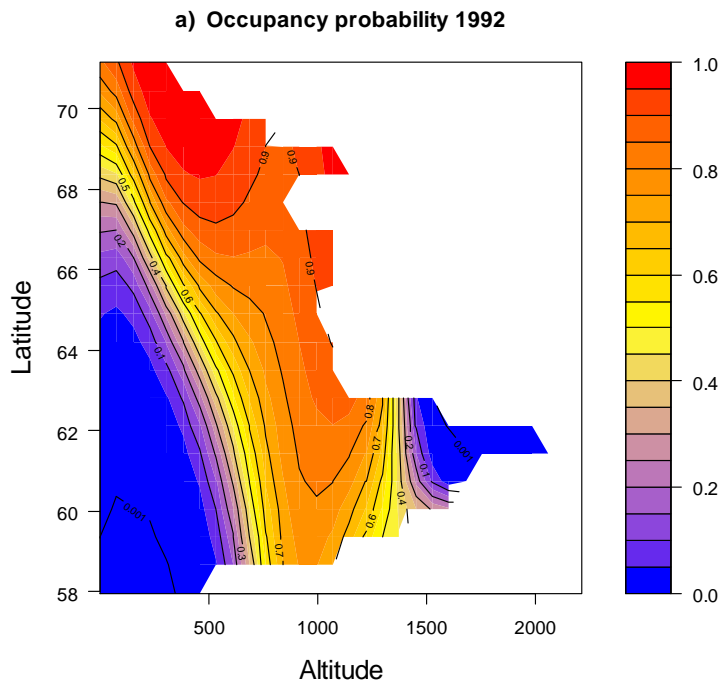


Figure A4. Model predictions of occupancy probability of Bluethroat as a combination of latitude and altitude in a) 1992 and b) 2002 (Model A).