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## Master thesis

Island biogeography along Norway's west coast - an explorative citizen science approach


A roe buck chasing a doe on the island of Hitra - the largest island in the study area. Photo: John D.C. Linnell

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#### Abstract

The theory of island biogeography is among the most recognized principles in the science of ecology. It states that the further away from the mainland, and the smaller an island is, the fewer species are present. Despite being one of the most island-rich countries worldwide, this theory has been poorly explored in Norway. Another important ecological principle, the latitudinal gradient of species richness, can be expected to be applicable to Norwegian islands due to the large latitudinal range of the Norwegian coast.

Here, online databases and questionnaires of knowledgeable local residents provided data. A framework consisting of rules was set to include study species and create relevant sampling units (archipelagos). The present study thereby aimed at exploring, and to a degree evaluating these mixed methods, as well as describing the contemporary biogeography of a subsample of Norway's oceanic islands.

Overall, number of species present on the islands was found to increase with size of the archipelago and decrease with distance to mainland and latitude. Results for predicting specific species' presence varied more. However, non-supportive results of the theory of island biogeography and the latitudinal gradient of diversity, were mostly explained by anthropogenic impact and species-specific habitat preferences. Additionally, the results suggested that local ecological knowledge was robust, although varying between species.

In conclusion, the theory of island biogeography and the latitudinal gradient of species richness is applicable to Norwegian islands, although the results should be interpreted with caution. The underlying dynamics in local knowledge are expected to be complex, and study species should be selected with care when using the present methods. This study provides a first approach on the topic, and further research is recommended to focus on countryside biogeography through human impact as well as habitat-related predictors.


Key words: Island biogeography, Latitudinal gradient, Rapoport's rule, Citizen science, Species distribution, Coastal ecology

## 1 Introduction

Explaining the variance within the complexity of nature has been a central goal of ecology since it emerged as a science, yet we are still struggling to achieve this (Møller \& Jennions, 2002). The ability of ecology to develop predictive theories is often discussed, especially in the context of rapid global change (Elliott-Graves, 2019). However, there are some predictive theories that stand strong and are continuously gaining more support. One of these is the theory of island biogeography, first proposed by MacArthur \& Wilson in 1963 and 1967, and tested by Simberloff in 1969 (MacArthur \& Wilson, 1967, 1963; Simberloff \& Wilson, 1969). In essence, the island biogeography theory states that the further away from the mainland, and the smaller an island is, the fewer species it contains (MacArthur \& Wilson, 1967). It changed the science of landscape ecology and has been recognized as one of the main principles in ecology (Brown \& Lomolino, 2000). Islands are of great interest in ecology, as they come in almost unlimited combinations of sizes, species compositions, biotic and abiotic compositions. Given the fact that they are isolated from the mainland to some extents, they have the potential to have unique ecosystems. Furthermore, they typically have simplified ecosystems and clear boundaries, making them easier to study (Harter et al., 2015). Notably, marine islands hold a disproportionately larger amount of the world's biodiversity (Russell \& Kueffer, 2019). They also have a high species turnover rate, and can therefore be expected to hold a high number of endemic species (Stuart et al., 2012). This high turnover rate makes marine islands fitting research objects, as they potentially can represent a glimpse into the future of our species and ecosystems, as well as allowing for research on species in unique food webs and ecosystems.

With a coastline of 100915 km and over 239000 islands, Norway has the second longest coastline, after Canada, and is among the countries with the most islands in the world (Regjeringen, 2021; Wikipedia, 2022). Since the human colonization at the end of the Ice Age the human use of the Norwegian coast in the form of fisheries has historically been, and still is, economically important for Norway (Aanesen et al., 2018; Arnesen et al., 2021; Løseth, 2019; Nærings- og fiskeridepartementet, 2021).

Additionally, harvesting of the land, including wild game and small scale agriculture, is viewed as a part of the Norwegian tradition (Miljødirektoratet, 2022; Øian \& Skogen, 2016). With traditions related to natural resource exploitation strongly embedded in the culture, and with Norway having this many islands, it could be expected that Norwegian islands have been well studied. Multiple ecological research projects have indeed been situated on Norwegian islands (Andersen et al., 1995; Hegland et al., 2021; Jacobsen \& Røv, 2007; Solberg et al., 2011). Surprisingly, the islands in themselves have, to our knowledge, rarely and only to a small extent been studied in an Island Biogeography setting (Costanzi \& Steifetten, 2019; Hatteland et al., 2008).

Another famous principle in macro-ecology, which has been acknowledged for a long time, is the latitudinal gradient of biodiversity (Wallace, 1854). This principle states that low latitudes have higher species richness than higher latitudes. The latitudinal gradient of biodiversity has been documented for a variety of taxa, including vertebrates (Gaston, 1996; Rabinovich \& Rapoport, 1975; Simpson, 1964; Willig et al., 2003). Given it's long length along a north-south axis it can be predicted that some latitudinal effects should be present in Norway, although one of the few existing studies, in the marine ecosystem, found no effect on this scale (Ellingsen \& Gray, 2002), despite the patterns being documented at larger scales (Rex et al., 2000).

Furthermore, Rapoport's rule (Stevens, 1989) relates to the latitudinal gradient of species richness and describes how species in high-latitude areas have wider latitudinal ranges than those of low-latitude areas. A suggested explanation is that species in high latitudes are exposed to a larger variety of seasonal climatic conditions and that they thereby are selected towards being latitude-generalists with high environmental tolerance (Letcher \& Harvey, 1994; Stevens, 1989). Regarding this, the dynamics of latitude in relation to species richness and presence can be expected to be less predictable for boreal or temperate species than for tropical species. Norway has high seasonal variance with a high temporal diversity of climatic conditions. Although the study area covers a wide range of latitudes, it is located within high-latitude areas. Therefore, Rapoport's rule would suggest that the species in this study should be present in a wide range of latitudes and have high environmental tolerance.

Given the long extent of human occupation and land use along the Norwegian coast it is also important to be aware of the potential human influence on ecosystems and species distributions through both deliberate and accidental introductions and eradications.

Despite the potential ecological insights that can be gained, there is major lack of research about species distributions and community structure from Norwegian island systems. The motivation for this thesis lies in the premise that an understanding of the broad scale distribution of species in the island environment along the coast of Norway will give valuable ecological knowledge and can potentially reveal useful considerations for wildlife management and biodiversity conservation.

Island biogeography theory, the potential influence of the latitudinal gradient principle, and human influence are natural starting points when studying a group of islands from an ecological point of view. The focus of this study was to conduct a preliminary survey of the broad scale distribution of a group of mammalian and avian species across a range of islands in central and western Norway. Limitations of time and budget forced this study to be based on a combination of pre-existing data from open-source databases (citizen science and wildlife management databases) and a telephone-based survey of local "experts" and residents of the islands. The approach used is a form of citizen science and an example of using local ecological knowledge. A consequence of this was that it was only possible to collect data in the form of presence / absence - the coarsest level of ecological information, and we could only do it for a set of species that are widely known and visible to local residents.

Accordingly, the study has focused on a set of species that include the most common huntable species or are otherwise well known and visible.

Therefore, this study has not only focused on providing a first approach by attempting to describe the contemporary biogeography of a set of Norwegian islands, but it also aimed at exploring the suitability of using citizen science methodology and evaluate it as thoroughly as possible with the information available. To describe island biogeography and diversity on Norwegian islands, as well as the validity of the method, the following specific questions were addressed:

- Does the theory of Island Biogeography apply to Norwegian islands? In other words, does probability of presence of the study species, and number of species present increase with increased size of the land area of the archipelagos and decrease with an increase in the archipelagos' distance to the mainland?
- Does the latitudinal gradient in species diversity apply to Norwegian islands? In other words, does probability of presence of the study species, and number of species present decrease with increased latitude?
- Do these patterns vary between species, depending on their ecology and their relationship with humans?
- To what extent is local ecological knowledge robust? In other words, how consistent are multiple informants and how does their knowledge compare to external data available from open-source databases?


## 2 Materials and methods

### 2.1 Study area

This study was conducted along the western coast of central Norway, between the southern border of Aukra municipality in the south and the northern border of Bodø municipality in the north. The area stretches approximately 673 km southwest - to northeast and varies in latitude between 62.75 and 67.70 degrees north. It was chosen because it covers a wide range of latitudinal degrees, represents a relatively consistent landscape structure with many islands, as well as that it is the stretch along the part of the coast which has the most known observations of the mammals and birds included in the study (according to data in the Norwegian Biodiversity Information Center's map service (Artsdatabanken, 2022)). Initially, the study area consisted of all municipalities with a coastline within these south/north borders ( $\mathrm{N}=$ 56). However, after analyses to select the sampling units (described in section 2.3.1


Figure 1. Map of the study area including the sampling units in red.

Archipelagos), the number of municipalities including sampling units, and therefore being included in the study area, was reduced to 29 (Figure 1).

The region is exposed to strong oceanic influences, which provide a very windy and exposed environment, but which also prevent the sea from freezing in winter. The islands consist of a diversity of habitats, depending on size and exposure, but typically contain a mix of smaller forest patches, exposed rocks, heather moorland, bogs, and agricultural land. Most islands of a size above a few square kilometers are occupied by humans, or at least contain buildings (Kartverket, 2021a).

### 2.2 Study species

14 species of mammals and birds varying in body size and taxonomy were chosen as study species. To ensure high validity in informants' response, visible and well-known species, most of which are huntable, were included. The study species were moose (Alces alces), red deer (Cervus elaphus), roe deer (Capreolus capreolus), red fox (Vulpes vulpes), pine marten (Martes martes), stoat (Mustela erminea), least weasel (Mustela nivalis), European badger (Meles meles), European hedgehog (Erinaceus europaeus), capercaillie (Tetrao urogallus), black grouse (Lyrurus tetrix), willow ptarmigan (Lagopus lagopus), red squirrel (Sciurus vulgaris), and mountain hare (Lepus timidus). All are known to occur on at least some islands, or the immediately adjacent mainland, within the study region(Artsdatabanken, 2022). Between them they represent a diversity of ecology, behaviour, habitat specificity, dispersal ability, and relationships with humans, which allows an exploration of the species specificity of the phenomena under investigation.

### 2.3 Sampling units

### 2.3.1 Archipelagos

The spatial analyses were based on the N50 map product, geodata from the Norwegian Mapping and Cadastre Authority (Kartverket, 2021a). In addition to N50, the vector layer landareal from the dataset Sjøkart - dybdedata was considered
(Kartverket, 2021b). The datasets were compared visually, N50 was found to contain more accurate details, and was therefore chosen as geodata.

In the study area, over 51000 islands ranging in size from less than a hectare to hundreds of square kilometers were identified through analysis in QGIS (QGIS Development Team, 2022). A set of criteria was then used to select islands and construct operational clusters, or "archipelagos", that would be large enough for the informants to be able to give good answers for, as well as narrowing the number of archipelagos down to a manageable number, while also providing a large range of island sizes, distances to the mainland and latitudinal degrees.

Firstly, islands smaller than $1 \mathrm{~km}^{2}$, or closer than 100 meters from the mainland were excluded on the grounds of being too small to support stable populations of the study species and not being sufficiently isolated as to constitute a real island. Secondly, islands closer than 500 meters from each other were grouped together to form archipelagos. Lastly, archipelagos with a total land area less than 2 square kilometers or visually surrounded by the mainland (e.g. inside sheltered fjords) were excluded. Archipelagos surrounded by mainland can potentially be part of migration routes, and the water surrounding them is expected to be calmer, as the mainland shelters them. By excluding them, the conditions for archipelagos included in the study were more similar and more consistently oceanic.

Furthermore, informants in this study provided more insight into making relevant island units for the investigation. In the first round of phone calls, one of the informants suggested to split one of the units into two units, as the two islands in the initial unit have different faunas (Stokkøya and Linesøya in Åfjord municipality). The two islands fulfilled the requirements considering minimum size and distance to mainland individually. They were also connected by recently constructed fill mass causeways on each side of the bridge. Without the fill mass, the two islands are located more than 1500 meters apart. The initial unit was therefore split and treated as two units in the subsequent steps.

The final set of sampling units consisted of 81 archipelagos ranging in size from 2 $\mathrm{km}^{2}$ to $610 \mathrm{~km}^{2}$ and located between 113 m and 40 km from the mainland, and from 62.82 to 67.40 degrees north.

### 2.3.2 Informants

The informants in this study were selected through an ad hoc quota sampling system, which can be defined as setting rules regarding number and traits of informants, then choosing the informants manually (Moser, 1952). Two informants were selected for each municipality in the study area, based on their employment positions or voluntary positions that associates them with local knowledge about the selected species. In total, 58 informants, distributed on 29 municipalities, provided data. From the first informant in each municipality, linear snowball sampling was conducted to get two sets of replies in the municipalities where only one of the initial informants' positions existed. The linear snowball sampling was done by asking the informants at the end of the survey who they thought could best answer the same questions, for the same municipality, with the highest accuracy possible. While it has been stated that snowball sampling is prone to bias (Bhardwaj, 2019), the risk of bias was minimized by asking the questions clearly and by remaining objective when talking to the informants. Additionally, the topic is not of a sensitive or personal nature, making the naming of a next informant from the first informant acceptable. In cases where the informants did not want to participate in the study, snowball sampling was applied to get a new informant.

To ensure the informants' anonymity, the rules for the quota sampling process is not described in further details.

### 2.4 Sampling

This study was conducted using a mixed methods approach, consisting of quota sampling, snowball sampling, phone call questionnaires and processing of opensource online data, and with the overall philosophy of using as many of the information sources that are available as possible. Sampling presence/absence data with the use of questionnaires has been done before (Berg et al., 1983; Pastorini et al., 2021; Reading et al., 1996). Additionally, one of the main purposes of the online databases used is to provide data for research (GBIF.org, 2022b). The individual methods in this study are in other words not novel. However, combining them in this way and in this context, has to our knowledge not been previously done in Norway.

### 2.4.1 Phone call survey

To gather the initial data, the informants (described in section 2.3.2 Informants) were contacted through phone calls and asked to answer an oral questionnaire (A1) during the phone call. Information on presence/absence of the study species, when and how the species came to the archipelagos, whether the archipelagos had a connection to the mainland, which type of connection it was and when it was connected was obtained from the informants. The question on how species came to the island was included to map the extent of direct human agency in shaping island community structure.

To combine the answers from the two respondents and to generate data on level of agreement between them, a set of rules was created. If the two informants answered the same, they agree and the result is "PRESENCE" if they both answered "YES", and "ABSENCE" if they both answered "NO". In cases where they both replied "I DON'T KNOW", the result was "NA". If one of them answered "I DON'T KNOW", the opinion of the other was put into the result column ("YES" = "PRESENCE" or "NO" = "ABSENCE"). In these cases, the level of agreement could not be decided, and was set to NA. If one respondent answered "YES" and the other answered "NO", it was noted as disagreement. However, the result would be considered as "PRESENCE". Since the species included are well known, and a "NO" potentially could mean "I've never seen it", a false positive is less likely than a false negative. Therefore, in cases where there was equal amounts of presence and absence, presence trumped absence in the decision tree (Table 1).

For cases where the archipelago was located on the border of two municipalities ( $\mathrm{N}=$ 3), answers from both municipalities were sampled, thereby potentially having four respondents for each archipelago. For determining level of agreement and presence/absence in these cases, the following rules were employed.

- If in the pool of answers one or more answered "YES" AND one or more answered "NO", they disagreed.
- If they all answered the same, they agreed.
- If there was one or more "YES" $\underline{\text { OR "NO", } \underline{\text { AND }} \text { one or more "I DON'T KNOW", they }}$ neither agreed nor disagreed and were set as NA's.
- Presence/absence was determined by what the majority answered, unless there were equal amounts of "YES" and "NO", in which case the result was set to "PRESENCE" due to false positives being less likely than false negatives.


### 2.4.2 Online datasets

Presence data for the study species from the last 20 years covering the municipalities of the study area was downloaded from GBIF (Global Biodiversity Information Facility) and Hjorteviltregisteret (Norwegian National Register for Cervids) (GBIF.org, 2022a; Naturdata, n.d.).

For the data from GBIF, coordinate uncertainty was set to 100 meters, one observation described as "preserved specimen" was excluded, and the final dataset downloaded from GBIF included 6235 observations from 6 datasets. After clipping the dataset by the study units, the dataset had 793 observations distributed on 42 of the 81 archipelagos.

Data on animals dying from other causes than hunting were downloaded from hjorteviltregisteret.no. The dataset included data on moose, red deer, roe deer, badger and red fox out of the species in this study. The initial dataset included 23679 observations in total, and after clipping it with the outlines of the archipelagos it ended up with 8112 observations distributed on 34 of the 81 archipelagos.

The two datasets combined, hereafter called "the online databases' dataset", had 8905 observations from 7 datasets. It contained observations of all the study species, except pine marten (13 of 14) distributed on 42 of 81 archipelagos.

### 2.4.3 Combining the datasets

Because the dataset from the informants contained presence/absence data and the online databases' dataset only contained presence, the latter could confirm presence, but not absence, from the first. The following rules were therefore set to combine the two datasets into the final dataset. When the informants' dataset had
"PRESENCE", the final dataset was set to "PRESENCE", regardless of what the online databases' dataset had. If the informants' dataset had "NA" and the online databases' dataset had "PRESENCE", the final dataset was set to "PRESENCE". In cases where both datasets had "NA", the final dataset was set to "NA" (Table 1). While the data from online databases is based on observations, the data from the informants is based on whether the species are permanently present, and the data from the informants was therefore considered to have a higher weight. Cases where the informants' dataset had "ABSENCE" and the online databases' dataset had "PRESENCE", were therefore associated with a high level of uncertainty. These cases were put in their own category to inspect how many of these cases the data contained. They were later classified as "NA's" because they represented only 8 out 1134 cases and because they did not provide good quality information.

### 2.5 Analyses

### 2.5.1 GIS analyses

The software QGIS 3.22.2 (QGIS Development Team, 2022) was used to select sampling units (described in section 2.3.1 Archipelagos) and to calculate land area of each archipelago and the latitude for individual archipelagos (sampling units). Distance to mainland was calculated as minimum distance between the polygon representing the mainland and each polygon representing the archipelagos through the analysis "near" in ArcGIS Pro 2.5 (Esri Inc., 2020). Land area of each archipelago was measured in square kilometers, latitude was measured in latitudinal degrees, and distance to mainland was measured in meters.

In addition, the software OpenJUMP with the analysis "make geometries valid" was used for processing of the geodata (The JUMP Pilot Project, 2008).

Table 1. Decision tree used to compare informants' answers and data from online databases and to create final datasets for analyses.

| Informant 1 |  |  | Informant 2 |  |  | Informants' dataset |  | Online databases |  | Final dataset |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| yes | no | I don't know | yes | no | I don't know | level of agreement | presence / absence | presence | NA | presence confirmed by online databases | presence <br> / absence |
| $\checkmark$ |  |  | $\checkmark$ |  |  | agree | presence | $\checkmark$ |  | confirmed | presence |
| $\checkmark$ |  |  | $\checkmark$ |  |  | agree | presence |  | $\checkmark$ | NA | presence |
|  | $\checkmark$ |  |  | $\checkmark$ |  | agree | absence | $\checkmark$ |  | not confirmed | presence |
|  | $\checkmark$ |  |  | $\checkmark$ |  | agree | absence |  | $\checkmark$ | NA | absence |
| $\checkmark$ |  |  |  | $\checkmark$ |  | disagree | presence | $\checkmark$ |  | confirmed | presence |
| $\checkmark$ |  |  |  | $\checkmark$ |  | disagree | presence |  | $\checkmark$ | NA | presence |
| $\checkmark$ |  |  |  |  | $\checkmark$ | NA | presence | $\checkmark$ |  | confirmed | presence |
| $\checkmark$ |  |  |  |  | $\checkmark$ | NA | presence |  | $\checkmark$ | NA | presence |
|  | $\checkmark$ |  |  |  | $\checkmark$ | NA | absence | $\checkmark$ |  | not confirmed | NA |
|  | $\checkmark$ |  |  |  | $\checkmark$ | NA | absence |  | $\checkmark$ | NA | absence |
|  |  | $\checkmark$ |  |  | $\checkmark$ | agree | NA | $\checkmark$ |  | NA | presence |
|  |  | $\checkmark$ |  |  | $\checkmark$ | agree | NA |  | $\checkmark$ | NA | NA |

### 2.5.2 Statistical analyses

Statistical analyses were conducted in Rstudio 2022.02.1 (R core team, 2022). Binomial models with three predictor variables (latitude, distance to mainland and size of archipelago) and presence/absence as response variable were built for each of the 14 study species. In addition, models with the same predictors and with number of species as the response variable were built to explore the basic elements of Island biogeography theory. Due to the data being right-skewed count-data, with overdispersion and mean unequal to variance, a negative binomial distribution was set for these models.

Since the study includes only three predictors, an all-subset approach was chosen, and all possible models $(\mathrm{N}=7)$ were built for each species and for number of species. Second-order Akaike's information criterion (AICc) was used to compare models. Due to high uncertainty in the AICc results, multi-model inference was conducted through full-model averaging and parameter weight utilized as a measurement for importance of parameters. All analyses were run for the dataset based on the informants' answers alone and for the final dataset. The results from the two datasets were compared visually.

Descriptive statistical analyses were conducted in, and presented through, Microsoft Office 365 (Microsoft Corporation, 2022) and Rstudio (R core team, 2022). The package Mumin (Bartoń, 2022) was used for second order AIC, model selection and model averaging, package DHARMa (Hartig, 2022) was used for model diagnostics, and packages tidyverse (Wickham et al., 2019) and ggplot2 (Wickham, 2016) were used to explore the data and plot the results.

## 3 Results

In total, presence/absence data for 14 species on 81 archipelagos was sampled from 58 informants and 7 online datasets. In the final dataset, the number of surveyed species present on the archipelagos varied between 0 (for the archipelagos Sørbuøya \& Nordøya, Børøya, Indre- \& Ytre Skjervøya and Søla) and 13 (for Averøya). The most common number of species present on the islands was 5 (Figure 2; A3).


Figure 2. Distribution of number of species on number of archipelagos in the study area.

### 3.1 Human-influenced presence of the study species

In $7.5 \%$ of the cases of presence, the informants reported that the species presence on the islands was due to human agency, either by crossing bridges or by being released by humans. badger was the species with the highest anthropogenic influence on presence, as it was reported as inhabiting the archipelagos by crossing bridges in $62,5 \%$ of the cases. Furthermore, mountain hare was the species being reported to have been released by humans the most (Figure 3).


Figure 3. Percentage-wise distribution of cases of human-influenced presence on the archipelagos out of the total number of presences for the study species, reported by the informants. Cases reported as the species inhabiting the archipelagos in a natural way or as "I don't know" are not included. The lowest bar represents the proportion of all presences across all study species which were reported to either be due to release or bridge-crossing.

### 3.2 Informants' dataset

Informant 1 and informant 2 agreed on average in $66 \%$ of all cases with the lowest agreement being $29.6 \%$ for stoat, and the highest being $92.6 \%$ for red deer. They disagreed on average in $5.8 \%$ of the cases, with the highest level of disagreement being $13.6 \%$ for stoat and the lowest being $0 \%$ for least weasel. The rest of the cases were not possible to classify as agreement or disagreement (Table 2).

In the informants' dataset, the species inhabited on average 28.4 archipelagos, with black grouse being present on the most archipelagoes ( $\mathrm{N}=62$ ) and least weasel being present on the fewest archipelagoes $(\mathrm{N}=2)$. The species where on average absent on 45.4
archipelagoes. Least weasel had the most cases of $N A(N=40)$, while red deer and moose had zero cases of NA (Table 2).

Table 2. Levels of agreement and presence/absence from comparing informants' answers.

|  | Agreement between informants in \% | Disagreement between informants in \% | $N$ of presence | $N$ of absence | $N$ of $N A$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Moose | 80.3 | 9.9 | 43 | 38 | 0 |
| Red deer | 92.6 | 7.4 | 18 | 63 | 0 |
| Roe deer | 85.2 | 3.7 | 46 | 34 | 1 |
| Red fox | 76.5 | 3.7 | 30 | 49 | 2 |
| Pine marten | 59.3 | 4.9 | 7 | 67 | 7 |
| Stoat | 29.6 | 13.6 | 50 | 16 | 15 |
| Least weasel | 59.3 | 0 | 2 | 39 | 40 |
| European badger | 75.3 | 3.7 | 8 | 72 | 1 |
| European hedgehog | 63 | 3.7 | 16 | 64 | 1 |
| Capercaillie | 72.8 | 6.2 | 14 | 58 | 9 |
| Black grouse | 50.6 | 6.2 | 62 | 16 | 3 |
| Willow ptarmigan | 71.6 | 6.2 | 61 | 15 | 5 |
| Red squirrel | 55.6 | 3.7 | 12 | 56 | 13 |
| Mountain hare | 51.9 | 8.6 | 28 | 48 | 5 |
| Mean | 66 | 5.8 | 28.4 | 45.4 | 7.3 |

Notes: Cases not possible to classify as agreement or disagreement (28.2\% on average) are not included in the table.

### 3.3 Informants' dataset and online databases' dataset

On average, online databases confirmed the presence from the informants' dataset in $10.3 \%$ of the cases. The highest percentage of confirmation was found for moose, with $30.9 \%$ of presence from informants' dataset being confirmed by online databases, while the lowest was found for pine marten and least weasel, with 0\% confirmed. In cases where informants' dataset indicated absence, the online datasets indicated presence in $0.7 \%$ of the cases on average. The highest number of these cases was found for red deer ( $3.7 \%$ ), while the lowest amount was found for 9 species ( $0 \%$ ) (Table 3).

The final dataset had an average of 28.5 presences and 44.8 absences per species. black grouse and willow ptarmigan were present on the most archipelagos ( $\mathrm{N}=62$ ), while least weasel was present on the fewest archipelagos $(\mathrm{N}=2)$. Least weasel had
the most NA's $(N=40)$, while moose and badger had the least NA's $(N=1)$ (Table $3)$.

Table 3. Presence from informants confirmed or not by online databases and presence/absence from the final dataset, made by comparing informants' and online databases' datasets.


| Moose | 30.9 | 1.2 | 43 | 37 | 1 |
| :--- | ---: | ---: | ---: | ---: | ---: |
| Red deer | 13.6 | 3.7 | 18 | 60 | 3 |
| Roe deer | 28.4 | 1.2 | 46 | 33 | 2 |
| Red fox | 14.8 | 2.5 | 30 | 47 | 4 |
| Pine marten | 0 | 0 | 7 | 67 | 7 |
| Stoat | 4.9 | 0 | 50 | 16 | 15 |
| Least weasel | 0 | 0 | 2 | 39 | 40 |
| European badger | 3.7 | 0 | 8 | 72 | 1 |
| European hedgehog | 7.4 | 1.2 | 16 | 63 | 2 |
| Capercaillie | 1.2 | 0 | 14 | 58 | 9 |
| Black grouse | 14.8 | 0 | 62 | 16 | 3 |
| Willow ptarmigan | 13.6 | 0 | 62 | 15 | 4 |
| Red squirrel | 2.5 | 0 | 13 | 56 | 12 |
| Mountain hare | 8.6 | 0 | 28 | 48 | 5 |
| Mean | 10.3 | 0.7 | 28.5 | 44.8 | 7.7 |
| N |  |  |  |  |  |

Notes: Cases not possible to classify as online databases confirming presence from informants or online databases indicating presence while informants indicate absence ( $89 \%$ on average), are not included in the table.

Comparing number of presences, absences and NA's for species individually between informants' dataset and the final dataset reveals that the two datasets are similar (Table 2; Table 3). Additionally, the structure regarding how many species are found on how many study units (Figure 2) was found to be identical between the datasets.

### 3.4 Island Biogeography analysis

Results from the island biogeography analyses produced from the informants' dataset only and from the final combined dataset were similar. In fact, the estimates for probability of presence of pine marten, stoat, least weasel, badger, capercaillie, black grouse, hare and number of species present were identical between the two datasets (Table 4; A2). Only results from the analyses of the final combined dataset will be presented/interpreted from here on, because the results were similar between the two datasets and because the last dataset includes data from multiple sources. Results from the analysis of the informant's only dataset can be found in Table A2 in the appendix.

For all species individually, the probability of presence increased with increased size of the archipelago. The probability of presence of hedgehogs and willow ptarmigan increased with increased distance to mainland, while the probability of presence decreased with increased distance to mainland for the rest of the species. Higher latitudes increased the probability of presence for moose, stoat, black grouse, willow ptarmigan and hare, but decreased the probability of presence for the other species (Table 4).

The size of the archipelago's land area was the most important predictor for probability of presence for 3 species, distance to mainland for 8 species, and latitude for 3 species. On the contrary, size of archipelago was the least important predictor for probability of presence for 4 species, distance to mainland was the least important predictor for 5 species, and latitude was the least important predictor for 5 species. (Table 4).

Overall, the number of species present on the archipelagos increased with increased size of the land area of the archipelago and decreased with increased distance to mainland and latitude. Latitude was the least important predictor for number of species present, while size of archipelago and distance to mainland were equally important (Table 4).

Table 4. Model-averaged estimates and parameter weights based on the final dataset for three variables on probability of presence of 14 species and on number of species present on archipelagos along the Norwegian coast between 62.75 and 67.70 degrees north.

|  |  | Intercept | Size of archipelago |  | Distance to mainland |  | Latitude |  | $\mathbf{R}^{2}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | estimate (SE) | estimate (SE) | weight | estimate (SE) | weight | estimate (SE) | weight | best model |
|  | Moose | - 3.94 (10.27) | 0.009 (0.0067) | * 0.84 | $\begin{aligned} & -9.3 \times 10^{-5} \\ & \left(3.8 \times 10^{-5}\right) \end{aligned}$ | ** 0.98 | $\begin{array}{r} 6.1 \times 10^{-7} \\ \left(1.4 \times 10^{-6}\right) \end{array}$ | 0.35 | 0.168 |
|  | Red deer | 105.65 (30.15) | 0.018 (0.0089) | * 0.96 | $\begin{aligned} & -1.3 \times 10^{-5} \\ & \left(3.4 \times 10^{-5}\right) \end{aligned}$ | 0.32 | $\begin{aligned} & -1.5 \times 10^{-5} \\ & \left(4.2 \times 10^{-6}\right) \end{aligned}$ | ** 1.00 | 0.569 |
|  | Roe deer | 59.15 (18.11) | 0.025 (0,0162) | 0.93 | $\begin{aligned} & -4.6 \times 10^{-5} \\ & \left(4.4 \times 10^{-5}\right) \end{aligned}$ | * 0.69 | $\begin{aligned} & -8.1 \times 10^{-6} \\ & \left(2.5 \times 10^{-6}\right) \end{aligned}$ | ** 1.00 | 0.325 |
|  | Red fox | 5.50 (10.97) | 0.004 (0.0056) | * 0.52 | $\begin{aligned} & -1.7 \times 10^{-4} \\ & \left(5.9 \times 10^{-5}\right) \end{aligned}$ | ** 1.00 | $\begin{aligned} & -7.1 \times 10^{-7} \\ & \left(1.5 \times 10^{-6}\right) \end{aligned}$ | 0.36 | 0.238 |
|  | Pine marten | 47.47 (41.08) | 0.011 (0.0083) | * 0.81 | $\begin{aligned} & -2.8 \times 10^{-3} \\ & \left(1.4 \times 10^{-3}\right) \end{aligned}$ | ** 1.00 | $\begin{aligned} & -6.6 \times 10^{-6} \\ & \left(5.7 \times 10^{-6}\right) \end{aligned}$ | 0.76 | 0.541 |
|  | Stoat | - 17.09 (22.40) | $\begin{array}{r} 1.9 \times 10^{-4} \\ (0.0023) \end{array}$ | 0.26 | $\begin{aligned} & -1.4 \times 10^{-4} \\ & \left(4.1 \times 10^{-5}\right) \end{aligned}$ | ** 1.00 | $\begin{array}{r} 2.7 \times 10^{-6} \\ \left(3.1 \times 10^{-6}\right) \end{array}$ | * 0.59 | 0.328 |
| Probability of presence | Least weasel | $\begin{array}{r} 271.28 \\ (189029.31) \end{array}$ | 0.413 (58.8922) | * 0.88 | - 0.08 (11.89) | ** 1.00 | $\begin{array}{r} -3.7 \times 10^{-5} \\ (0.03) \end{array}$ | 0.24 | 1 |
|  | European badger | 73.56 (33.65) | 0.002 (0.0037) | 0.48 | $\begin{aligned} & -8.7 \times 10^{-4} \\ & \left(4.9 \times 10^{-4}\right) \end{aligned}$ | ** 0.99 | $\begin{aligned} & -1.0 \times 10^{-5} \\ & \left(4.7 \times 10^{-6}\right) \end{aligned}$ | * 0.97 | 0.375 |
|  | European hedgehog | 49.38 (24.81) | 0.025 (0.0076) | ** 1.00 | $\begin{gathered} 3.3 \times 10^{-5} \\ \left(4.6 \times 10^{-5}\right) \end{gathered}$ | 0.49 | $\begin{aligned} & -7.2 \times 10^{-6} \\ & \left(3.5 \times 10^{-6}\right) \end{aligned}$ | * 0.94 | 0.488 |
|  | Capercaillie | 41.005 (26.66) | 0.005 (0.0053) | 0.65 | $\begin{aligned} & -7.1 \times 10^{-4} \\ & \left(3.2 \times 10^{-4}\right) \end{aligned}$ | ** 1.00 | $\begin{aligned} & -5.7 \times 10^{-6} \\ & \left(3.7 \times 10^{-6}\right) \end{aligned}$ | * 0.85 | 0.429 |
|  | Black grouse | - 12.23 (18.44) | $\begin{gathered} 9.8 \times 10^{-4} \\ (0.0034) \end{gathered}$ | 0.30 | $\begin{aligned} & -1.1 \times 10^{-4} \\ & \left(3.5 \times 10^{-5}\right) \end{aligned}$ | ** 0.99 | $\begin{gathered} 2.0 \times 10^{-6} \\ \left(2.6 \times 10^{-6}\right) \end{gathered}$ | * 0.54 | 0.220 |
|  | Willow ptarmigan | - 69.35 (21.16) | 0.019 (0.0121) | * 0.93 | $\begin{gathered} 4.7 \times 10^{-5} \\ \left(5.9 \times 10^{-5}\right) \end{gathered}$ | 0.57 | $\begin{array}{r} 9.7 \times 10^{-6} \\ \left(2.9 \times 10^{-6}\right) \end{array}$ | ** 1.00 | 0.302 |
|  | Red squirrel | 29.34 (28.03) | 0.022 (0.0077) | ** 1.00 | $\begin{aligned} & -1.3 \times 10^{-4} \\ & \left(9.4 \times 10^{-5}\right) \end{aligned}$ | * 0.85 | $\begin{aligned} & -4.3 \times 10^{-6} \\ & \left(3.9 \times 10^{-6}\right) \end{aligned}$ | 0.72 | 0.510 |
|  | Mountain hare | - 5.51 (10.55) | 0.012 (0.0053) | ** 0.99 | $\begin{aligned} & -1.0 \times 10^{-6} \\ & \left(1.5 \times 10^{-5}\right) \end{aligned}$ | 0.26 | $\begin{gathered} 6.2 \times 10^{-7} \\ \left(1.5 \times 10^{-6}\right) \end{gathered}$ | * 0.35 | 0.115 |
| N species | Number of species | 4.83 (3.32) | 0.002 (0.0005) | ** 1.00 | $\begin{aligned} & -3.1 \times 10^{-5} \\ & \left(7.8 \times 10^{-6}\right) \end{aligned}$ | ** 1.00 | $\begin{aligned} & -4.4 \times 10^{-7} \\ & \left(4.6 \times 10^{-7}\right) \end{aligned}$ | 0.62 | 0.548 |

Notes: $\mathrm{R}^{2}$ was derived from the best model according to AICc, pre-averaging. ${ }^{* *}=$ most important predictor, ${ }^{*}=$ second most important predictor.

## 4 Discussion

### 4.1 Island biogeography and latitudinal gradient of diversity

The results suggested that the theory of island biogeography and the latitudinal gradient of diversity applies to Norwegian islands overall, albeit the latter to a lower degree than the first (Table 4). Estimates for the species individually varied in terms of the relative importance of the different variables and how the variables predicted the species' probability of presence. All the study species were more likely to be present on the larger archipelagos, but the relationships regarding distance to mainland and latitude were of a more complicated nature.

For three of the study species, latitude was the most important variable for predicting the probability of presence; red deer and roe deer appeared less likely to occur further north, and willow ptarmigan appeared more likely to occur further north. This was not surprising, since red deer and roe deer have been expanding northwards from refuges in southwestern Norway and southern Sweden respectively. It therefore reflects their ongoing population expansion (Andersen et al., 2004; Haanes et al., 2008), which has only modestly been influenced by direct human assistance. Willow ptarmigan prefers tundra and mountainous habitat (Johnsgard, 1983), which is more common further north, as the tree line is of lower altitude and the trees are smaller. Additionally, and contrary to the principle of the latitudinal gradient of biodiversity, the probability of presence of moose, stoat, black grouse and hare also increased with increased latitude.

While species richness was explained by latitude, this parameter appears to be of least importance compared to distance to mainland and size of the archipelagos, according to parameter weights (Table 4). This result is contradictory, as, according to Rapoport's rule, species richness should not be explained by latitude due to the hypothesis that our study species should be present across a large range of latitudes (Stevens, 1989). On the other hand, support for Rapoport's rule is found in the fact that this parameter is of least weight (Table 4). This suggests that both the latitudinal gradient of species richness and Rapoport's rule are supported by the results. In general, it is discussed whether the two principles have similar underlying causes on
a global scale (Stevens, 1989). However, when including fewer latitudinal degrees, especially when the study area is further from the equator, a more unclear relationship can be expected, as seen in Rapoport's rule. The species in this study can potentially have ranges stretching throughout the whole study area (supported by their mainland distributions), and so the latitudinal gradient of species richness would be less detectable. This can potentially contribute to the explanation of why the latitude-presence relationship is inconsistent in the results from this study.

For most species ( $\mathrm{N}=8$ ), distance to mainland was the most important predictor for probability of species presence. The probability of presence decreased with increased distance to the mainland for all species, except for the hedgehog and willow ptarmigan, for both of which it surprisingly increased with increased distance to mainland. This latter result does not correspond with the theory of island biogeography, albeit we can argue that distance to mainland was the least important predictor for these two species.

Hedgehogs are known to be frequently moved and released by humans, also in Norway (Jackson et al., 2004; Poléo, 2012). In fact, the informants in this study reported hedgehog as the second most released species (Figure 3). Hedgehogs can swim, but with the currents and waves of the ocean, it is logical to assume that when a hedgehog occurs on an archipelago, it has most likely been released by humans at some point during the millennia of occupation.

Intraguild predation between hedgehogs and badgers has been reported, with hedgehogs occurrence decreasing when badger occurrence increases (Hof et al., 2019). The most important predictor for probability of presence of badgers in this study was distance to mainland, and they are more likely to be found closer to the mainland. If we further assume that hedgehogs have been moved and released extensively on the islands along the Norwegian coast, the badgers may potentially have had a negative impact on the hedgehogs' survival on the islands closer to the mainland, and so the hedgehogs may have had a higher survival rate on the islands further away from the mainland.

As mentioned earlier, willow ptarmigan was more likely to be present further away from the mainland. This can potentially be explained by avian species' ability to fly and that the distance to the mainland therefore would be of less importance in
influencing their initial colonization. The results show that distance to mainland was the least important predictor for probability of presence of willow ptarmigan, but they also show that it was the most important predictor for probability of presence of the two other avian species, black grouse and capercaillie (Table 4). Additionally, the results suggests that black grouse and capercaillie are less likely to be present further away from the mainland. Black grouse and capercaillie are typically found in, or in proximity to, forest habitat, while willow ptarmigan prefers more open areas such as alpine tundra, with low shrubs and few trees (Johnsgard, 1983). Considering this, a possible explanation for the increased probability of presence of willow ptarmigan further away from the mainland is that archipelagos further away from the mainland are more exposed, and that the habitat in these areas therefore more resembles the habitat found in alpine tundra or moorland (mediated by wind exposure rather than altitude). This pattern in vegetation in relation to the distance from the mainland can also potentially explain why moose are less likely to be found further away from the mainland, even though they are good swimmers; in 2005 a single moose was observed in Træna municipality, where the island of Sanna, the sampling unit furthest away from the mainland ( 40 km ) is located (NRK, 2005). Moose have also naturally colonized the island of Vega, one of the sampling units, located 11 km from the mainland (Sæther et al., 2001). Because moose are associated with forest habitats, both for foraging and cover (Bjørneraas et al., 2011), it is as expected that they are less likely to be found further away from the mainland. In addition to hedgehogs, four other species were reported to have been intentionally released by humans. While red deer, roe deer and red fox have only a few cases of release, mountain hares were reported to have been released in half of the cases in which they were noted as present (Figure 3). As an example, mountain hares were reported to have been released on the largest sampling unit in the study, consisting of the island of Hitra and the smaller islands around ( $610 \mathrm{~km}^{2}$ ). This sampling unit makes up for a major part of the terrestrial area of Hitra municipality, which has more than 5200 inhabitants (Statistics Norway, 2022). It is therefore not surprising that the presence of species is influenced by humans in this unit. Breeding and releasing of mountain hares by humans on Norwegian islands is a well-known phenomenon; it has mainly been done by hunters, based on the thought that the local hare populations on islands suffer from inbreeding and need human assistance to stay
healthy (Huseby \& Bø, 1986; Pedersen \& Pedersen, 2012). Introduction of red deer and roe deer in Norway is less common, but it has been done. In fact, a well-known case is the translocation and release of 17 German-Hungarian red deer on Otterøya, close to the study area, between 1900 and 1903 (Haanes et al., 2010; Skavhaug, 2005). These results are in other words as expected, and the fact that mountain hare presence has been directly influenced by humans to a high degree can potentially explain why the ecological models for mountain hare have the least statistical power ( $\mathrm{R}^{2}=0.115$; Table 4).

Another way in which humans influence the species that can inhabit the archipelagos, is through the species crossing bridges from the mainland. Bridges longer than 100 meters between the mainland and the sampling units are extensively present in the study area (The Norwegian Public Roads Administration, n.d.). This way of species arrival was reported for two species, mountain hares and badgers, although the presence of mountain hares was only reported in one case. However, badgers were reported to have inhabited the islands by crossing bridges in more than half of the cases (Figure 3).

Together, the results indicate that island populations of badgers and mountain hares are highly influenced by humans through indirect and direct mechanisms, respectively. Overall, the presence of populations of the study species were mentioned as human-influenced in $7,5 \%$ of the cases (Figure 3). However, this should be considered as a minimum number as the informants answered "I don't know" in many cases. Further, exploration of "countryside biogeography", defined as " the study of the diversity, abundance, conservation, and restoration of species in rural and other human-dominated landscapes (Daily, 1997; Daily et al., 2001)" in the study area appears as an opportunity when the observed patterns of species' distribution are related to a combination of both natural and human-modified processes. The motivations for deliberate species introduction, especially for a species like hedgehogs, could also be of great interest to explore.

### 4.2 Local ecological knowledge

The results from comparing informants' answers to each other and to online databases indicate that the informants possessed robust local ecological knowledge. The amount of agreement measured against the amount of disagreement between the informants shows that informants agreed 11 times more often than they disagreed (Table 2). Comparison of informants' answers and data from online databases reveals that in cases where online databases have "presence", informants' dataset has "presence", on average, 14 times more often than "absence" (Table 3). This can to a large degree indicate that the local knowledge is accurate, or at least consistent with independent data.

The level of agreement between the informants also varied between the species. Unsurprisingly, moose, red deer and roe deer have the highest proportions of agreement and mountain hare, black grouse and stoat have the lowest proportion of agreement. The cervids have large body sizes, are often visible when feeding on agricultural fields, are culturally well-known species, and are popular huntable game species, often hunted in teams of multiple landowners. The local residents are therefore expected to have solid knowledge about these species. On the contrary, mountain hare, black grouse and stoat are smaller body size species which makes them less visible, and thus, knowledge about them might be lower among local residents. However, in our study, the variance of informants' agreement level does not have a clear and consistent pattern. As an example, the level of agreement for the study species with the smallest body size, least weasel, is higher than for mountain hare, black grouse and stoat. In addition, it is the only species with no cases of disagreement between the informants. The underlying dynamics for level of agreement between the informants can thereby be expected to be of high complexity, which suggests that when sampling presence/absence data through questionnaires in this context, one should choose study species, informants, and sampling units with caution, and be aware of economic, recreational, cultural and social aspects of the species' relationships with people.

### 4.3 Limitations and possible improvements

Like all studies conducted using indirect and opportunistic data from very large study areas there are limitations. These limitations are related to uncertainty in the models and low number of informants per sampling unit, and the rules set to create the sampling units.

When including few predictors, a potential risk is a decrease in the ability to explain the variance in the data. In this study only three predictors were included in the models, resulting in varying statistical power, shown by the coefficient of determination ( $\mathrm{R}^{2}$ ) for the best models (Table 4). As highlighted by the informant's answers, variables connected to human settlements might contribute to increasing statistical power of the models, as human influence has been shown for species' presence (Figure 3).

Because of limited time and interview personnel available, the number of informants was restricted to two per sampling unit, with the potential risk of a weaker basis for evaluating local knowledge. Through increasing the number of informants per sampling unit, more solid data could be obtained, and the results could be interpreted with higher confidence. However, it could also be expected that increasing the number of informants would increase the level of disagreement between them concerning many species, especially the more cryptic species. This would make interpretation more complex.

Another potential source of bias that is important to address is the subjective nature of the rules set to create operational sampling units. These rules were set on the bases of multiple tradeoffs; for example, islands closer than 500 meters from each other were merged, while minimum distance to mainland was set to 100 meters. These decisions allowed for retainment of the "distance to mainland" variable and ensured that size of the sampling units was large enough for informants to give high quality answers. Preferably, the minimum distance between the islands merged should be equivalent to the distance between the sampling units and the mainland, when assuming they share the same fauna. However, the dependence on being able to access the local knowledge of residents required the use of units that
corresponded to a scale, and orientation, of geographic precision to which the informants could relate.

While this study brings light to an unexplored area of research, the results should be interpreted with a certain caution. To minimize limitation biases from this study, further research should be conducted with the following recommendations. The influence of number of informants and rules set to create archipelagos should be explored. Additionally, the potential anthropogenic impacts on the biogeography of Norwegian marine islands should be assessed to a higher degree through the inclusion of variables on human settlement, human modification of habitat, and human activities.

### 4.4 Conclusion

The results from this study suggests that both the island biogeography theory and the latitudinal gradient of biodiversity are broadly applicable to Norwegian islands. However, the patterns of how the variables influence the probability of presence of the individual study species vary. In addition, a substantial amount of the variation in predicting presence/absence of the species is not explained by the variables included, which indicates that there might be other important predictors. Moreover, anthropogenic impacts influenced a large proportion of the cases of presence. Further research should explicitly investigate the role of further variables in predicting the number of species present or the presence of specific species. These should include human settlement, human activity, land use and forest types, amongst others. Because of the direct and indirect roles of humans in both colonization and persistence of species, the emerging countryside biogeography framework, that explicitly integrates anthropogenic and ecological influences, offers productive avenues. Knowledge regarding countryside biogeography may further provide valuable insight for wildlife management and stakeholders, as humans substantially influence, and alter, their surrounding ecosystems.

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## APPENDICES

A1: Questionnaire used for sampling of presence/absence data. The questions were asked for each species and for each archipelago.

## Introduction of topic and information

My name is Jørgen Henden, and I am doing a master's degree in Applied Ecology. The thesis is revolving around island biogeography on Norwegian islands, and I am focusing on these fourteen species (mention each species). The method is to contact local people that are expected to have knowledge about theses species' local distribution. It is $100 \%$ anonymous and will take approximately X minutes (based on how many sampling units are located in the municipality). When the results are ready, I will make a summary and send it to the informants who are interested. In that context, I am wondering if you would be willing to answer this questionnaire?

## Questionnaire

1. Is there a connection between the archipelago and the mainland, and if so, which type? (bridge, tunnel, ferry, none)
2. If yes, when was the connection made?
3. For each species:
a. Is this species present on the archipelago? (yes, no, I don't know)
b. When did this species inhabit the archipelago?
c. How did the species inhabit the archipelago?
4. Do you want me to contact you again when I have written the summary so that you can see the results?

A2. Model-averaged estimates and parameter weights based on informants' answers for three variables on probability of presence of 14 species and on number of species present on archipelagos along the Norwegian coast between 62.75 and 67.70 degrees north.

|  |  | Intercept | Size of archipelago |  | Distance to mainland |  | Latitude |  | $\mathrm{R}^{2}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | estimate (SE) | estimate (SE) | weight | estimate (SE) | weight | estimate (SE) | weight | best model |
|  | Moose | -2.87 (9.20) | 0.009 (0.0066) | 0.85 | $\begin{aligned} & -9.3 \times 10^{-5} \\ & \left(3.8 \times 10^{-5}\right) \end{aligned}$ | 0.98 | $\begin{gathered} 4.6 \times 10^{-7} \\ \left(1.3 \times 10^{-6}\right) \end{gathered}$ | 0.32 | 0.168 |
|  | Red deer | 103.26 (29.07) | 0.017 (0.0078) | 0.97 | $\begin{aligned} & -8.8 \times 10^{-6} \\ & \left(2.9 \times 10^{-5}\right) \end{aligned}$ | 0.29 | $\begin{aligned} & -1.5 \times 10^{-5} \\ & \left(4.1 \times 10^{-6}\right) \end{aligned}$ | 1.00 | 0.539 |
|  | Roe deer | 55.62 (16.96) | $0.003(0,0059)$ | 0.46 | $\begin{aligned} & -7.3 \times 10^{-5} \\ & \left(4.1 \times 10^{-5}\right) \end{aligned}$ | 0.90 | $\begin{aligned} & -7.5 \times 10^{-6} \\ & \left(2.3 \times 10^{-6}\right) \end{aligned}$ | 1.00 | 0.268 |
|  | Red fox | 3.28 (8.43) | $\begin{array}{r} 7.8 \times 10^{-5} \\ (0.0015) \end{array}$ | 0.25 | $\begin{aligned} & -1.7 \times 10^{-4} \\ & \left(5.9 \times 10^{-5}\right) \end{aligned}$ | 1.00 | $\begin{aligned} & -4.0 \times 10^{-7} \\ & \left(1.2 \times 10^{-6}\right) \end{aligned}$ | 0.31 | 0.187 |
|  | Pine marten | 47.47 (41.08) | 0.011 (0.0083) | 0.81 | $\begin{aligned} & -2.8 \times 10^{-3} \\ & \left(1.4 \times 10^{-3}\right) \end{aligned}$ | 1.00 | $\begin{aligned} & -6.6 \times 10^{-6} \\ & \left(5.7 \times 10^{-6}\right) \end{aligned}$ | 0.76 | 0.541 |
|  | Stoat | - 17.09 (22.40) | $\begin{gathered} 1.9 \times 10^{-4} \\ (0.0023) \end{gathered}$ | 0.26 | $\begin{aligned} & -1.4 \times 10^{-4} \\ & \left(4.1 \times 10^{-5}\right) \end{aligned}$ | 1.00 | $\begin{array}{r} 2.7 \times 10^{-6} \\ \left(3.1 \times 10^{-6}\right) \end{array}$ | 0.59 | 0.328 |
| Probability of presence | Least weasel | $\begin{array}{r} 271.28 \\ (189029.31) \end{array}$ | 0.413 (58.8922) | 0.88 | - 0.08 (11.89) | 1.00 | $\begin{array}{r} -3.7 \times 10^{-5} \\ (0.03) \end{array}$ | 0.24 | 1 |
|  | European badger | 73.56 (33.65) | 0.002 (0.0037) | 0.48 | $\begin{aligned} & -8.7 \times 10^{-4} \\ & \left(4.9 \times 10^{-4}\right) \end{aligned}$ | 0.99 | $\begin{aligned} & -1.0 \times 10^{-5} \\ & \left(4.7 \times 10^{-6}\right) \end{aligned}$ | 0.97 | 0.375 |
|  | European hedgehog | 46.99 (24.84) | 0.024 (0.0074) | 1.00 | $\begin{gathered} 2.0 \times 10^{-5} \\ \left(3.6 \times 10^{-5}\right) \end{gathered}$ | 0.40 | $\begin{aligned} & -6.9 \times 10^{-6} \\ & \left(3.5 \times 10^{-6}\right) \end{aligned}$ | 0.93 | 0.487 |
|  | Capercaillie | 41.005 (26.66) | 0.005 (0.0053) | 0.65 | $\begin{aligned} & -7.1 \times 10^{-4} \\ & \left(3.2 \times 10^{-4}\right) \end{aligned}$ | 1.00 | $\begin{aligned} & -5.7 \times 10^{-6} \\ & \left(3.7 \times 10^{-6}\right) \end{aligned}$ | 0.85 | 0.429 |
|  | Black grouse | - 12.23 (18.44) | $\begin{array}{r} 9.8 \times 10^{-4} \\ (0.0034) \end{array}$ | 0.30 | $\begin{aligned} & -1.1 \times 10^{-4} \\ & \left(3.5 \times 10^{-5}\right) \end{aligned}$ | 0.99 | $\begin{gathered} 2.0 \times 10^{-6} \\ \left(2.6 \times 10^{-6}\right) \end{gathered}$ | 0.54 | 0.220 |
|  | Willow ptarmigan | - 72.0 (21.49) | 0.019 (0.0115) | 0.94 | $\begin{gathered} 3.8 \times 10^{-5} \\ \left(5.4 \times 10^{-5}\right) \end{gathered}$ | 0.51 | $\begin{gathered} 1.0 \times 10^{-5} \\ \left(3.0 \times 10^{-6}\right) \end{gathered}$ | 1.00 | 0.311 |
|  | Red squirrel | 28.29 (27.68) | 0.021 (0.0082) | 0.99 | $\begin{aligned} & -1.5 \times 10^{-4} \\ & \left(1.0 \times 10^{-4}\right) \end{aligned}$ | 0.87 | $\begin{aligned} & -4.2 \times 10^{-6} \\ & \left(3.8 \times 10^{-6}\right) \end{aligned}$ | 0.70 | 0.484 |
|  | Mountain hare | - 5.51 (10.55) | 0.012 (0.0053) | 0.99 | $\begin{aligned} & -1.0 \times 10^{-6} \\ & \left(1.5 \times 10^{-5}\right) \end{aligned}$ | 0.26 | $\begin{gathered} 6.2 \times 10^{-7} \\ \left(1.5 \times 10^{-6}\right) \end{gathered}$ | 0.35 | 0.115 |
| N species | Number of species | 4.83 (3.32) | 0.002 (0.0005) | 1.00 | $\begin{aligned} & -3.1 \times 10^{-5} \\ & \left(7.8 \times 10^{-6}\right) \end{aligned}$ | 1.00 | $\begin{aligned} & -4.4 \times 10^{-7} \\ & \left(4.6 \times 10^{-7}\right) \end{aligned}$ | 0.62 | 0.548 |

Notes: $R^{2}$ was derived from the best model according to AICc, pre-averaging. ${ }^{* *}=$ most important predictor, ${ }^{*}=$ second most important predictor.

A3. Presence (yes), absence(no) and NA for the study species on the archipelagos in the study area.

| Islands in the archipelago | moose | red <br> deer | roe <br> deer | $\begin{array}{\|l\|} \hline \text { red } \\ \text { fox } \\ \hline \end{array}$ | pine marten | stoat | least weasel | european badger | european hedgehog | capercaille | black grouse | willow ptarmigan | red squirrel | hare |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Gossa | yes | yes | yes | NA | no | no | no | no | yes | no | yes | no | no | no |
| Averøya | yes | yes | yes | yes | yes | yes | yes | yes | yes | yes | yes | yes | yes | no |
| Flatsetøya, Frei, Nordlandet, Gomalandet, Kirklandet | yes | yes | yes | yes | no | yes | no | no | yes | yes | yes | yes | no | no |
| Golma, Gautøya, Tustna, Stabblandet, Solskjels $\varnothing$ ya | yes | yes | yes | yes | yes | yes | NA | yes | no | yes | yes | no | yes | no |
| Ertvågs $\varnothing$ ya, Rottøya | yes | yes | yes | yes | yes | yes | NA | yes | no | yes | yes | NA | yes | yes |
| Grisvågøya, Lesundøya, Skardsøya | yes | yes | yes | yes | yes | yes | NA | yes | yes | yes | yes | NA | yes | NA |
| Edøya, Kuli | no | yes | no | no | no | no | no | no | yes | no | no | yes | NA | yes |
| Smøla, Rossvolløya, Jøa, Kvalpøya, Måøya, Kråkøya | no | yes | NA | no | no | no | no | no | yes | no | no | yes | yes | yes |
| Røstøya | yes | yes | yes | yes | NA | NA | NA | no | no | yes | yes | yes | NA | NA |
| Hitra, Jøsnøya, Straumøya, Gjøssøya, Helsøya, Helgbustadøya, Hjertøya, Dolmøya | yes | yes | yes | NA | no | yes | no | no | yes | yes | yes | yes | yes | yes |
| Olderøya, Burøya (Bispan) | no | yes | yes | no | no | yes | no | no | no | no | NA | NA | no | yes |
| Fjellværsøya, Ulvøya | no | yes | yes | no | no | yes | no | no | NA | no | NA | yes | no | yes |
| Sørleksa, Nordleksa | no | yes | yes | no | no | no | no | no | no | no | yes | yes | no | yes |
| Storfosna | no | NA | yes | yes | no | yes | no | yes | yes | no | yes | no | NA | yes |
| Tarva | no | no | no | no | no | yes | no | no | yes | no | no | no | NA | yes |
| Været | no | no | no | no | no | yes | no | no | no | no | no | no | NA | no |
| Frøya, Dola, Uttian, Rottingen, all islands out to Sørdyrøya | no | yes | yes | no | no | no | no | no | yes | no | no | yes | no | yes |
| Inntian | no | no | no | no | no | no | no | no | yes | no | no | yes | no | no |


| Sørburøya, Nordøya | no | no | no | no | no | no | no | no | NA | no | no | NA | no | no |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Linesøуa | no | NA | yes | no | no | NA | NA | no | no | no | yes | yes | NA | no |
| Stokkøya | yes | no | yes | yes | no | NA | NA | yes | no | no | yes | yes | NA | no |
| Børøуa | no | no | NA | no | no | NA | NA | no | no | NA | NA | no | NA | no |
| Ytre og Indre Skjervøya | no | no | no | no | no | no | no | no | no | no | no | no | no | no |
| Нepsøуa | no | no | yes | no | no | no | no | no | no | no | no | no | no | no |
| Ramsøya | no | no | yes | no | no | yes | no | no | no | no | yes | no | no | no |
| Aspøya, Halmøуa | no | no | yes | yes | no | yes | NA | no | no | yes | yes | no | NA | no |
| Kvernøya | yes | yes | yes | yes | yes | yes | NA | no | no | yes | yes | no | yes | no |
| Bjørøya | yes | yes | yes | yes | no | yes | NA | no | no | yes | yes | no | yes | no |
| Inner-, ytter-, mellomVikna, marøya, nærøya, lauvøya | yes | no | yes | yes | yes | yes | yes | yes | yes | no | yes | yes | yes | no |
| Vågøya/Svinøya | yes | no | yes | yes | no | yes | NA | no | no | no | yes | yes | NA | no |
| Gjerdinga | yes | no | yes | yes | no | yes | NA | no | no | no | yes | yes | no | no |
| Kalvøya/Borgan | yes | no | yes | yes | no | yes | NA | no | no | no | yes | yes | no | no |
| Kvaløуa | yes | no | yes | yes | no | yes | NA | no | no | no | yes | yes | no | no |
| Raudøуa | no | no | yes | NA | no | yes | NA | no | no | no | yes | yes | no | no |
| Dolma | yes | no | yes | NA | no | yes | NA | NA | no | no | yes | yes | no | no |
| Leka | no | no | yes | no | no | yes | NA | no | no | no | yes | yes | NA | yes |
| Torget, Sauren, Stortorgnes, Helløya, Ormøya | yes | no | yes | yes | NA | yes | NA | no | no | yes | yes | yes | yes | yes |
| Vega, Igerøya | yes | no | yes | no | no | no | no | no | yes | no | yes | yes | yes | yes |
| Ylvingen | yes | no | no | no | no | no | no | no | no | no | no | no | no | no |
| Søla | no | no | no | no | no | no | no | no | no | no | no | no | no | no |
| Hamnøуa | yes | no | yes | yes | NA | yes | NA | no | no | no | no | yes | no | no |
| Mindland | yes | no | yes | no | no | NA | NA | no | no | NA | yes | yes | yes | no |
| Tro, Rødøya/Flatøya | yes | no | yes | no | no | NA | NA | no | no | NA | yes | yes | no | no |
| Rosøya | yes | no | yes | no | no | NA | NA | no | no | NA | yes | yes | no | no |
| Alstenøya, Alsta/Tjøtta | yes | yes | yes | yes | no | yes | NA | yes | yes | yes | yes | yes | yes | yes |


| Blomsøy, Austbø | yes | no | yes | no | no | NA | NA | no | no | NA | yes | yes | no | no |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Herøy, Dønna | yes | NA | yes | no | no | yes | no | no | yes | no | yes | yes | no | yes |
| Skorpa | no | no | yes | no | no | yes | no | no | no | no | yes | yes | no | yes |
| Havstein/Vandve to Lamøya | yes | no | yes | no | no | yes | no | no | no | no | yes | yes | no | yes |
| Slapøуa | yes | no | yes | no | no | yes | no | no | no | no | yes | yes | no | yes |
| Løkta | no | no | yes | no | no | yes | no | no | no | no | yes | yes | no | no |
| Hugla | yes | no | no | no | no | yes | NA | no | no | no | yes | yes | no | yes |
| Tomma | yes | no | no | yes | no | yes | NA | no | no | no | yes | yes | NA | yes |
| Handnesøya | yes | no | no | yes | no | yes | NA | no | no | no | yes | yes | no | yes |
| Sanna | no | no | no | no | no | no | no | no | no | no | no | yes | no | no |
| Виøуа | no | no | no | no | no | no | no | no | no | no | yes | yes | no | no |
| Straumøya, Ulvøya, Lunderøya, Svenningen | no | no | no | no | no | no | no | no | no | no | yes | yes | no | no |
| Lovund | no | no | no | no | no | no | no | no | no | no | yes | yes | no | no |
| Lurøya, Onøya, Stigen | yes | no | no | no | no | yes | no | no | no | no | yes | yes | no | no |
| Aldra | Yes | no | no | yes | no | yes | no | no | no | yes | yes | yes | no | yes |
| Indre Kvarøy | no | no | no | no | no | yes | no | no | no | no | yes | yes | no | no |
| Storselsøya | yes | no | no | no | no | yes | no | no | no | no | yes | yes | no | no |
| Nesøya | yes | no | no | no | no | yes | no | no | no | no | yes | yes | no | no |
| Rangsundøya, Selsøya and everythin between | no | no | no | no | no | yes | no | no | no | no | yes | yes | no | no |
| Sundøya | no | no | no | no | no | yes | no | no | no | no | yes | yes | no | no |
| Renga | no | no | no | no | no | yes | no | no | no | no | yes | yes | no | no |
| Gjerdøya | no | no | no | no | no | yes | no | no | no | no | yes | yes | no | no |
| Rødøуа | yes | no | no | no | no | yes | no | no | no | no | yes | yes | no | no |
| Åmøya, Grønnøya, Hestøya, Storøya | yes | no | yes | yes | no | yes | NA | no | no | yes | yes | yes | no | yes |
| Bolga | no | no | yes | yes | no | yes | NA | no | no | NA | yes | yes | no | NA |
| Meløya, Skjerpa, Mesøya | yes | no | yes | yes | no | yes | NA | no | no | NA | yes | yes | no | yes |
| Teksmona | yes | no | no | yes | no | yes | NA | no | no | NA | yes | yes | no | yes |
| Støtt | no | no | no | yes | no | yes | NA | no | no | NA | yes | yes | no | NA |


| Sandhornøуa | yes | yes | yes | yes | yes | yes | NA | no | no | no | yes | yes | no | yes |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Femris | yes | no | yes | yes | NA | NA | NA | no | no | no | yes | yes | no | no |
| Fugløya | no | no | no | no | NA | NA | NA | no | no | no | yes | yes | no | no |
| Fleina | NA | no | no | no | NA | NA | NA | no | no | no | yes | yes | no | NA |
| Sør-Arnøya og NordArnøya | yes | no | no | no | NA | NA | NA | no | yes | no | no | yes | no | no |
| Bliksvær | no | no | no | no | no | NA | NA | no | no | no | no | yes | no | yes |
| Store Hjartøya | no | no | no | yes | no | NA | NA | no | no | no | no | no | no | no |
| Landegode | no | no | no | no | no | NA | NA | no | no | no | yes | yes | no | yes |

