

Island Biogeography of small mammals in Denmark: Effects of area, isolation and habitat diversity

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M.Sc. Thesis

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Cover photo: *Apodemus sylvaticus*, one of the most abundant rodents in Denmark

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Abstract

The distribution of 12 mammal species of the genera *Rodentia* and *Insectivora* were investigated by trapping and gathering of information on 31 Danish islands covering a wide range of sizes and distances to the mainland. The aim was to elucidate which factors determine the total number of small mammal species on each island and the distribution of each of these species.

No island were found to hold all species and a nested species distribution pattern showed that there is differences in both dispersal abilities of species and their extinction risk once present on an island. Isolation proved to have a negative effect on total number of species and on the presence of 5 species. Area had no direct effect on the number of species but was found to be positively correlated with island diversity, represented by total number of habitats and the Shannon index. Island diversity had a positive effect on total number of species and on the presence of two species. For the distribution of four of the twelve species no variables showed significant explaining power.

Introduction

For more than 200 years biologists have known that islands harbour fewer species of animals and plants per area unit than their mainland counterparts. One of the first to report this was J. R. Forster, who travelled as a naturalist on the ships of the world renowned explorer James Cook (Lomolino, 2001). Many of the later studies were also often performed on the great ship explorations of that time. These showed that not only do islands hold fewer species than mainland, but also that the diversity of these islands increased with island size and available resources (Lomolino, 2001)

The growing amount of studies led to the need for an explanation of this pattern that was observed again and again. Many researchers offered their version of which factors influences the distribution, dispersal and extinction of animals and plants. These explanations were largely qualitative and most often dealt with individual species or groups of species, for example birds (Lack, 1976) ignoring the total number of species. A quantitative theory that could be tested in the field did not arrive until 1967, when MacArthur and Wilson published their Theory of Island Biogeography. In this they hypothesised that the number of species on an island is in equilibrium between immigration and extinction, and that the immigration rate will vary with the distance of the island to the mainland and the extinction rate with the area of the island. MacArthur and Wilson (1967) were not the first to put forward this idea of an equilibrium. Preston did this already in 1962 (Preston, 1962a),(Preston, 1962b), but they were the first to develop the idea in a simple mathematical form (Williamson, 1983). MacArthur and Wilson's mathematical theory was based on studies of many different kinds of organisms, from plants and invertebrates to birds and land vertebrates (MacArthur & Wilson, 1967), but the main part of their data originated from studies on land and freshwater birds on oceanic islands because those data were readily available (Hanski, 1986).

There are enormous differences in dispersal and colonisation abilities of organisms and thus their speediness in obtaining equilibrium on the islands. Therefore most of the enormous amount of research their theory prompted has been made on birds, land plants and good invertebrate dispersers who presumably obtain equilibrium fast. Much interest has been devoted to elucidating which factors are most important to the presence or absence of organisms on islands and systematic differences have been discovered. Schoener et al. (1986) showed that vertebrates generally are more affected by island area than invertebrates, and

that the invertebrates are more sensitive to distance effects than vertebrates, but nearly all the vertebrates included in their paper were birds and lizards. This corresponds well with MacArthur and Wilson's original findings, but again most of the included data were from bird studies (MacArthur & Wilson, 1967).

However, there has been some research done specifically on mammals. In 1948 Hatt and Tyne investigated the fauna on the Islands of Lake Michigan, USA and suggested several theoretical explanations as to why a mammal species is present or absent on an island. These included the age of the island, its size and the variation of habitat types (Hatt & Tyne, 1948). They also emphasised distance to nearest island or mainland but made no concluding remarks as to which factors were the most important determinant of island mammal fauna.

In 1971 Brown tested the general applicability of the equilibrium theory for non-oceanic islands. He came to the conclusion that boreal mammals on mountaintops in the Great Basin, USA were most affected by the size of their "island" and not significantly by the distance to the mainland, i.e. Rocky Mountains (Brown, 1971). Vertebrates of Georgian Bay Islands National Park, North Eastern USA behaved similarly (Schmiegelow & Nudds, 1987). 70% of the variation in species number on these islands was explained by area. Brown excluded large carnivores and ungulates from his study, but included small predators and rodents (Brown, 1971) and Schmiegelow and Nudds (1987) included all non volant mammals.

The question is whether this area relationship holds true if only the smallest mammals, the rodents and the shrews, are included. These small mammals have the presumably poorest colonisation ability, but are they also more affected by area than by any isolation effects? More than 70% of the variation in rodent species number on small islands around New Zealand was found to be explained by island area (Yom-Tov et al., 1999). However, the rodents studied were all invasive species brought along on ships and therefore presumably not affected by distance.

Lomolino (1982) suggested that the apparent unimportance of distance in determining number of mammal species on islands in some studies (Brown, 1971), (Duesser & Brown, 1980) is due to the narrow range in isolation values of the chosen study sites compared to the limited dispersal powers of terrestrial mammals. This is taken into account by Adler and Wilson (1985) who analysed the small mammal assemblages on a group of islands off the

coast of Massachusetts, USA. They include islands situated from less than 50 m off the coast till nearly 38 km off the coast and they found contrary to Brown (1971) that only half of the small mammal species were most affected by island size, whereas the distribution of the other half was mostly affected by isolation (Adler & Wilson, 1985). Adler and Wilson have not been the only ones to get results which differ depending on the species or island. Grant compared rodent distribution on three archipelagos in England, Canada and Denmark (Grant, 1970). He found significant correlations between species number and isolation in UK and Canada but a non-significant relationship between species and island area. In Denmark he found significant relationships between both isolation and area. Grant used data collected by Ursin (1950). These data did not cover all the Danish islands, but only the South Funen Archipelago.

Size and isolation of an island are not the only factors affecting species richness. Habitat diversity may in fact be much more important and more direct in exerting its effects on fauna diversity. Early in their book MacArthur and Wilson (1967) write: “Our ultimate theory of species diversity may not mention area, because area seldom exerts a direct effect on a species’ presence. More often area allows a large enough sample of habitats, which in turn control species occurrence”. They continue to mention that only the absence of good information on diversity of habitats made them turn to area. The difficulty in obtaining good measures of habitat diversity has resulted in virtually all island biogeography studies being focused on the effects of area and not habitats. Adler and Wilson (1985) define total number of major habitat types and the dominant type in their study. The dominant habitat type comes out as significant variable for two species, but neither they nor any of the studies mentioned here have made any other attempts to quantify island habitat diversity (Grant, 1970), (Hatt & Tyne, 1948), (Brown, 1971), (Lomolino, 1984 (review)).

Therefore an attempt to analyse whether the area effects observed in most of the aforementioned studies in reality are effects of habitat diversity would be interesting.

An omission in MacArthur and Wilson’s theory of island biogeography (MacArthur & Wilson, 1967) is its failure to deal with the historical aspect of an island’s biota. Their original theory did not deal with the fact that many islands are landbridge islands, i.e. the island was in the past connected to the mainland. Brown (1971) states that only in the absence of

historical perturbations and speciation will the number of species on an island represent an equilibrium between the opposing rates of extinction and immigration. He finds in his study of boreal small mammals that these communities cannot be described by the equilibrium theory. He finds that they are relict faunas that colonized their mountain tops during the last connection of these with the “mainland” and which later have only experienced extinctions and no immigrations (Brown, 1971).

Case and Cody (1987) also suggest that MacArthur and Wilson’s theory may not always be qualified to explain the fauna distribution patterns of islands, especially for such slow colonisers as rodents and other small mammals. If the species turnover on an island is fast, i.e. the colonisation and extinction events occur rapidly as in birds, then the historical legacy of an island may be erased fast and equilibrium attained earlier. This would make it indistinguishable whether an island is oceanic starting out with no species, or a landbridge island starting out with all the same species as the mainland pool (Case & Cody, 1987). For the less able colonisers like mammals the slow turnover might make the time needed to attain equilibrium so long that it is never reached.

Most Danish islands are landbridge islands, which within the last 10.000 years have been connected to the mainland. Most were isolated from the mainland by the coming of the Littorina Sea approximately 8000 years ago (Hansen, 1994), (Aaris-Sørensen, 1998). This coming was caused by the melting of the last of the North American ice shield, and resulted in a 25 m rise in sea level over a period of 500 years (Andersen & Sjørring, 1997). The islands that are surrounded by deep waters today were those isolated first by the rising sea and those with shallow waters around them were isolated later. This is especially true for the South Funen archipelago. There are quite shallow waters between these islands and they are south of the line that divides Denmark into a northern and southern part. A northern part that rises after being released from the pressure of the ice of the last ice age, and a southern part that is depressed accordingly. Thus for a long time after the littorina transgression they still made up one large landmass. Only with the continuing depression of southern Denmark was this landmass fragmented into islands.

A few of the Danish islands have never been connected to the mainland in their present form, but are built up by sand depositions by the sea. These could be considered oceanic

islands and include Læsø and Fanø. Another island that has never been connected to the mainland is Egholm near Aalborg. It was earlier a part of the seabed and has only come into existence by the continuing rising of the land in northern Denmark. However when the weather conditions are right Egholm becomes almost connected to the mainland (see appendix 3).

This mixture of landbridge and oceanic islands in the Danish archipelago should make it possible to test Case and Cody's (1987) predictions that small mammal assemblages will need more than 10.000 years to reach equilibrium. This could be done by testing if there is a difference in the number of species on the oceanic islands and the landbridge islands. Registrations of the mammal fauna on smaller Danish isles are more than 50 years old (Ursin, 1948b), (Ursin, 1952a) but does not cover all islands. To my knowledge only one attempt to quantify factors important to the mammal distribution on Danish islands has been made, and this only covers a fraction of the islands (Grant, 1970).

An interesting question is thus which factors are the most important determinants of the composition and size of the small mammal fauna on the Danish isles. Are Grant's (1970) results from the South Funen archipelago valid for all islands? The 13 South Funen islands in Grant's study range in size from 150 ha to 29.000 ha but in Denmark there are more than 400 islands varying in size from tiny sandbanks less than one ha to the more than 7000 km² large Zealand. They are also extremely different in their degree of isolation. Some are only situated a few meters from an adjacent mainland, whereas others are 45 km from the nearest mainland. Studies of birds and island biogeography in Denmark isles would probably reveal no variation, since most of the islands are within easy reach of most birds. With the less able mammal dispersers however the Danish islands seem to offer an ideal setup.

In this study only rodents (*Rodentia*) and shrews (*Insectivora*) are included. Some of these immigrated to Denmark shortly after the ice retreated and the latest arrival has only been here for about two hundred years but together these species comprise a broad range of ecotypes from strict folivores over granivores to carnivores. The rodents included in this study are all of the family *Muridae* but divided into two subfamilies. The *Arvicolinae* subfamily comprises the voles and lemmings, and is represented in Denmark by four species. Three of them, the bank vole (*Clethrionomys glareolus*, Schr.), the water vole (*Arvicola terrestris*, L.) and the field vole (*Microtus Agrestis*, L.) are fairly abundant and distributed all over the country. The

common vole (*Microtus arvalis*, Pallas) is only found in Jutland with decreasing density to the north. The field- and the common vole are both predominantly grass eaters, and live mostly in different types of meadows or in forest glades where there is a good grass cover (Manniche, 1935). The water vole is mostly found on tidal meadows and in hedgerows (Ursin, 1948a). The last of the Danish voles, the bank vole is associated with forests and other small tree covered habitats. Consequently, it is not a specialised grass eater but prefers nuts and grains (Manniche, 1935).

The other subfamily, the *Murinae* includes rats and mice and is represented in Denmark by five species. The two species most strongly connected with human activity, the house mouse (*Mus musculus*, L.) and the brown rat (*Rattus norvegicus*, Erxleben) are very abundant and widely distributed in Denmark wherever humans are. They are also some of the latest arrivals in Denmark. Two other common mice in Denmark are the yellow necked mouse (*Apodemus flavicollis*, Melchior) and the wood mouse (*Apodemus sylvaticus*, L.). The wood mouse is found in almost every type of habitat, but where it occurs in the same places as the yellow necked mouse it is ousted by it and forced away from the yellow necked mouse's favourite habitats which are mature forests, parks and other tree covered places. The last of the mice and the smallest rodent in Denmark is the harvest mouse (*Micromys minutus*, Pallas). It is the latest known arrival in Denmark and a very good disperser, with and without the help of man. It was recorded on Zealand less than 100 years from its first being recorded in southern Jutland.

The last three species of small mammals are shrews (*Insectivora*). The common shrew (*Sorex araneus*, L.) and the pigmy shrew (*Sorex minutus*, L.) are found in many different habitats and both require a dense vegetation cover (Winge, 1908). The European water shrew (*Neomys fodiens*, Pennant) has a preference for wetlands near streams, ponds and lakes, especially where the plant cover along the brink is good (Carlsen, 1995).

The aim of this study is to elucidate which factors decide the presence of rodents and shrews on the islands of the Danish archipelago. The importance of area and isolation is tested. In addition habitat diversity is quantified in an effort to distinguish between regular area effects and diversity effects. This analysis is applied to all species combined and to each species separately in order to investigate if the same variables affect all species equally or their response varies.

Study sites

31 Danish islands are included in this study. Islands and their location are shown in figure 1. They vary a lot in size from 2.5 ha to more than 58.000 ha and with distances to the mainland ranging from a few hundred meters to 45 km. Most of the Danish islands including those in this study are dominated by agriculture, since this is one of the few activities that are still economically viable on islands. On several of the included islands

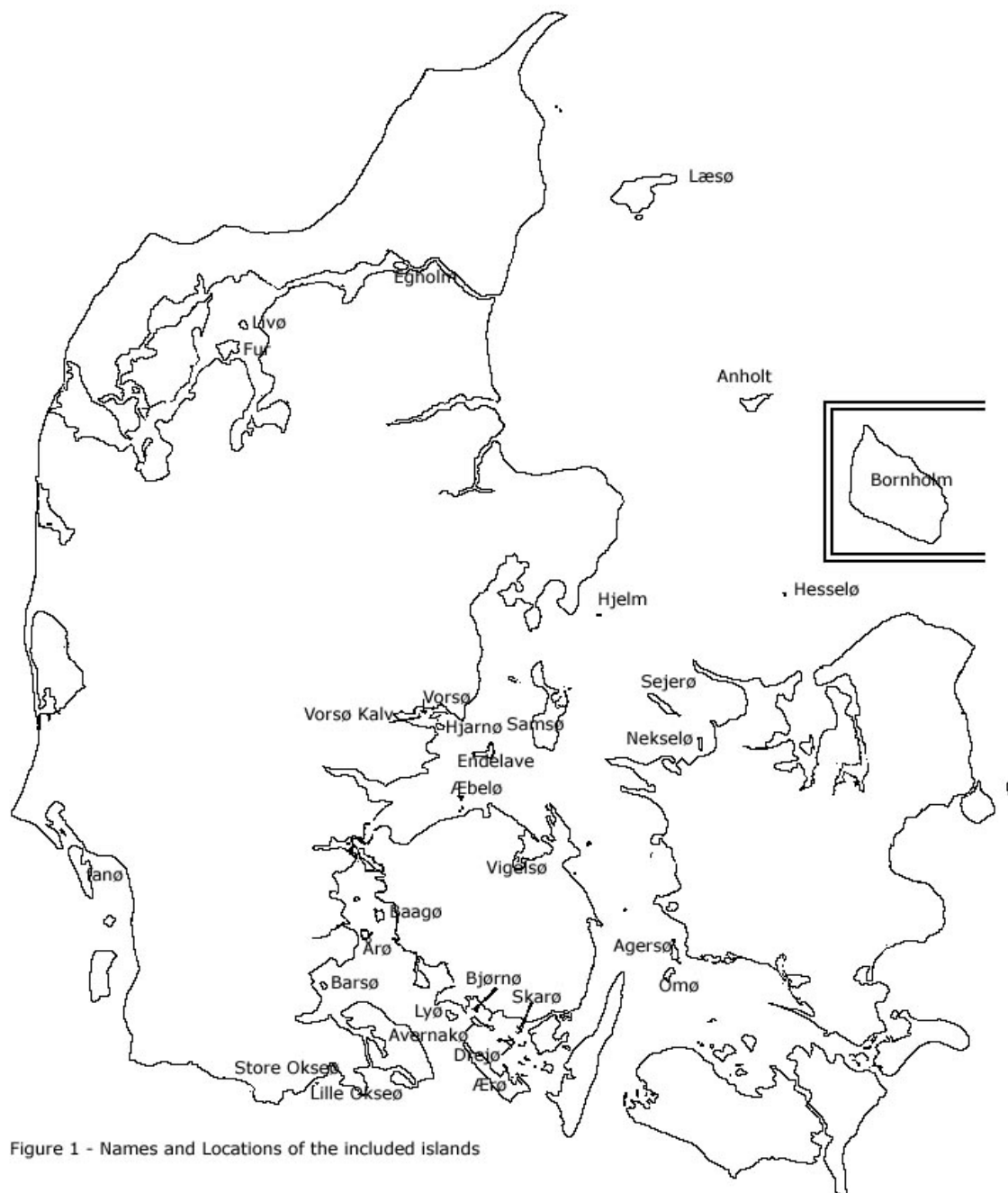


Figure 1 - Names and Locations of the included islands

more than 2/3 of the land is cultivated and on many of the larger islands agriculture dominates occupying about 45% of the land or more. See appendix 1 for full information on the amounts of farmland and other nature types on each island. Only on the smallest or most isolated islands like Anholt there are no longer any farmers. Some of the smallest islands are owned by the state or private foundations, e.g. Vigelsø, Vorsø, Vorsø Kalv and Æbelø. On many of the other islands parts of the land are protected by legislation (see Methods for further description). The proportion protected on each island varies widely from zero to more than 90%.

Most of the islands in the inner seas are fertile with profitable farming, but two of the “oceanic” islands in this study, Læsø and Fanø, have poor sandy soils and only smaller areas are cultivated. Instead they are covered by large areas of moors and plantations planted to prevent soil erosion. Anholt, which is also mainly built up by the sea like Læsø and Fanø, has almost ¾ of its land covered by moors.

Forests and other kinds of wood-covered areas are not protected and many of the islands have considerably less wood cover than the 12% average for the entire country (Statistics Denmark, 2005). The amount of wood cover varies from less than 5% to more than 60% and these numbers even include hedgerows and other small biotopes not included in the national statistics. There is no general pattern on the agricultural islands, but islands without farm land have considerably more wood cover than the other islands.

Among the protected vegetation types are tidal meadows, which many of the islands abound in. They cover up to 25% of the area, but there is seemingly no pattern that explains the differences in amount of tidal meadows with regards to island size or the amount of other vegetation types.

Only five of the islands in this study are uninhabited. The rest have from one to just under 44.000 permanent residents. The population density varies from one person per 50 ha to one per 1.25 ha. Ærø and Bornholm are the most densely populated islands and generally the smaller the island the thinner the population. This has several reasons, but the main one being the lack of jobs and educational opportunity. There are large differences though. Islands with frequent ferry connections to the mainland and short crossing times generally also have the most people. There are exceptions though. Egholm with ferries every half hour throughout the day and five minutes to the centre of Aalborg has only 60 inhabitants, whereas Agersø of

similar size have more than four times as many inhabitants but also four times the distance to the mainland and half as many ferry connections.

Table 1. Demographic data from the islands.

Island	Size (ha)	Number of inhabitants	Distance to nearest mainland (m)	Distance to Jutland or Germany (m)	Age (years)
Agersø	684	255	2200	93000	8000
Anholt	2237	157	45000	45000	8000
Avernakø	586	121	3300	33000	4000
Barsø	266	25	1700	1700	8000
Bjørnø	150	33	700	33000	4000
Bornholm	58744	43956	37000	37000	10250
Baagø	623	35	3000	6800	7500
Drejø	426	72	6400	35500	4000
Egholm	600	52	450	450	5000
Endelave	1308	177	9500	9500	7500
Fanø	5578	3169	1300	1300	5000
Fur	2229	939	600	600	8000
Hesselø	71	2	25000	50000	8000
Hjarnø	321	119	800	800	7000
Hjelm	70	0	4900	4900	8000
Ll. Okseø	3,5	0	350	350	7500
Livø	331	8	4000	4000	8000
Lyø	605	146	2100	26000	6000
Læsø	10122	2228	20500	20500	2700
Nixelø	223	24	1150	53000	8000
Omø	452	193	5700	87500	8000
Samsø	11206	4421	11000	11000	7500
Sejerø	1237	387	8500	35000	8000
Skarø	197	39	1800	42000	4000
St. Okseø	7,8	0	500	500	7500
Vigelsø	120	0	300	41200	7500
Vorsø	56	1	550	550	7000
Vorsø Kalv	2,5	0	1300	1300	7000
Æbelø	209	2	1000	10000	8000
Ærø	8807	7050	11500	25500	4000
Årø	566	204	550	550	7500

Although most of the islands are dominated by agriculture most of them have a varied predator fauna. More than half of the investigated islands houses red fox (*Vulpes vulpes*) and many also the small mammal predators weasel (*Mustela nivalis*) and stoat (*Mustela erminea*). In addition to the natural Danish predators, American mink (*Mustela vison*) is present as an escaped farm animal with a breeding population on Læsø. On all the inhabited islands except

Æbelø and Vorskø there are also domestic cats. There are no cats on any of the uninhabited islands. For complete data on predators, see appendix 2.

Birds of prey have been observed on all islands in this study, either as stationary breeding birds or as migrant visitors. The most commonly observed birds of prey are the common buzzard (*Buteo buteo*) and the kestrel (*Falco tinnunculus*).

The climate in the Danish archipelago is temperate coastal climate with cool summers and mild winters. The average temperatures are 0.0°C in February and 15.7°C in August. The average yearly precipitation is 712 mm (Statistics Denmark, 2005). The East Jutland islands and those in the Great Belt area enjoy a slightly warmer and drier climate than the rest of country because the predominantly westerly winds in Denmark dumps most of their moisture in Jutland.

Methods

Islands

The human population size data on the 31 islands were supplied by Statistics Denmark (Statistics Denmark, 2005). Data about numbers of inhabitants are from January 1st 2003. Where more recent data were available from the island residents, these were used. Distance from island to the mainland was measured from the mapping services provided by the Danish counties on the internet (Fyns-Amt et al., 2004).

Information on mammal predators and birds of prey were from different sources, including my own observations, information from residents and reports to the project Danish Mammal Atlas from 2000-2003 (Dansk Pattedyr Atlas, 2003).

Information about the islands geological history was mostly from the literature (Aaris-Sørensen, 1998), (Hansen, 1994), (Nørrevang, 1967), (Pedersen et al., 1997) and personal communication with Niels Tvis Knudsen, Institute of geology, University of Aarhus.

Several practical considerations had an impact on which islands were included in the data set. There had to be some kind of public transport and accommodation. Part of the funding to this project came from the Danish Mammal Atlas Project (Dansk Pattedyr Atlas, 2003). Therefore islands of interest to that project were visited first. My goal was to get as wide a range of island sizes and distances to the mainland as possible.

On two islands with no forms of public transportation, there was no trapping done, and the information was supplied second hand. Information on the fauna of Hesselø was found in the literature. On Hjelm information was supplied by Jørgen Terp Laursen (Teacher and volunteer at the Natural History Museum, Aarhus). Not all of the other islands were visited by me personally. These were either visited by trained biologists from the Natural History Museum in Aarhus or by very able amateur biologists (Ole Bang Nielsen, contributor to the Mammal Atlas).

To determine the habitat diversity of each island the amount of §3 protected land was determined from maps provided on the internet by the Danish counties (Fyns-Amt et al., 2004). §3 refers to the Danish law “Bekendtgørelse af lov om naturbeskyttelse” (LBK nr 884 dated 18/08/2004), which states that, there cannot be made any changes in the state of

moors, bogs, tidal meadows, meadows and biological commons, if any of these nature types alone or together have an area that is larger than 2500 m². It also protects natural lakes larger than 100m², and streams can be appointed for protection.

These §3 registrations were combined with aerial photos of the islands. These photos and registrations were imported into the computer photo editing program Photoshop 6.0 (Adobe, 2000), where the rest of the area of each island were appointed to one of four categories, tree-covered land, permanent grassland, buildings and cultivated land. This was done by marking the areas with different colours. Then the computer was used to calculate the percentages of each category on each island.

Mice

Denmark has 17 species of small mammals. Of these five are not included in this study. One of these, the house rat (*Rattus rattus*), is extinct or very close to extinction, with only very few scattered occurrences (Jensen, 1993). The newly arrived muskrat (*Ondatra zibethicus*), which was observed for the first time in southern Jutland in 1989, is not included either. Three other species have only regional distributions in Denmark and are therefore not relevant in this study. The northern birch mouse (*Sicista betulina*) is only found in Thy and the upper part of western Jutland. According to old information it also occurs in southern Jutland, but this needs to be confirmed. The hazel dormouse (*Muscardinus avellanarius*) is only found on southern Funen and has a few isolated occurrences on Zealand. The striped field mouse (*Apodemus agrarius*) occurs only on Lolland-Falster. None of these three species have been observed on any of the islands included in this study.

In Denmark there are two kinds of house mouse. Earlier they were considered two races of the same species (*Mus musculus musculus* and *M. m. domesticus*). Now many consider them as separate species (*Mus musculus* & *Mus Domesticus*) (Jensen, 1993). Their appearance and behaviour are quite alike though, and they are therefore treated as one species here.

Data collection

Field work was conducted from October 2002 until August 2004. Permission to collect mice was obtained via The Mammal Atlas project. With few exceptions each island was visited for three days each, i.e. putting out the traps and leaving them to stand for two nights. This means that on most islands the number of trap nights are the number of traps times two. The traps used in this study are Swedish Ugglan type traps, which is a live capturing trap,

made of wire netting. The traps were baited with oats and apple and hay were used for nesting material. The traps were placed in lines of ten traps each, alternating between traps with a large opening and trapdoor and traps with a small opening and trapdoor. The traps were where possible placed in a straight line with 15 steps between each trap. When traps were placed near water, the line followed the edge of the water rather than a straight line. This mode of operation was chosen because it is the same as used in the Mammal Atlas project for catching small mammals (Dansk Pattedyr Atlas, 2003).

On each island the trap lines were placed geographically as varied as possible according to where permission to trap had been obtained from landowners. My aim was to cover the widest possible variety of nature types, while at the same time reflecting the extent of the various nature types with the distribution of the trap lines.

When tending the traps the following data were noted from each catch: species, date, trap number, trap line number, whether the specimen was dead or alive, and with live specimens, whether they were let loose or brought back for further examination.

Statistics

The statistical software used in all tests was JMP, version 5.0.1.2 (SAS, 2002). The percentages of nature types on each island were used to calculate habitat diversity indices for each island. The indices used were the Shannon-Weaver index (Begon et al., 1996) and the Simpson index (Begon et al., 1996).

$$\text{Shannon-Weaver Index } H = -\sum P_i \cdot \ln P_i$$

$$\text{Simpson Index } D = 1/\sum P_i^2$$

Parametric tests are the most powerful in statistics but also make the strongest assumptions, some of them being that the observations must be independent and be drawn from populations that are normally distributed. Therefore all data in this study were tested for normality and where this was not the case transformation of the data was tried, either logistic or other functions, for example $x+1$. The Shapiro-Wilkes test (SAS, 2002) was used to test the data's goodness of fit to a normal distribution and where the data were tested against the log normal distribution the Kolmogorov-Smirnoff test was used (Sokal & Rohlf, 1995).

The normal or log-normally distributed parameters were tested for correlation with the parametric pairwise correlation test (SAS, 2002). Those variables that have values slightly lower than 5% were also tested with the non-parametric Spearman-rank correlation test (SAS, 2002) to ascertain that the deviation from the log-normal distribution were not critical.

The relationship between numbers of species and explanatory variables was estimated by multiple stepwise regression (backwards selection). The probability to enter was 0.1 and probability to leave 0.05.

The relationship between the presence-absence of each species and the explanatory variables was estimated with logistic regression. Again the probability to enter was 0.1 and probability to leave 0.05. When the significant variables for each species were decided, these were entered in a fit Y by X model (SAS, 2002). An example of the resulting datasheet is given in Figure 2.

The overall probability to encounter *At* (*Arvicola terrestris*) on an island are depicted in the right side of the figure, represented by the 1 part of the axis. Over the regression line are the islands where *A.terrestris* is present and under it those where it is absent. The estimate for “Ln distance to nearest mainland” represents the slope of the regression line and since it is positive in this example the result is that the longer the distance to the mainland, the smaller the probability of encountering *A.terrestris*. Thus the curve can be used to estimate the probability of encountering the species on any island within the Danish archipelago which falls within the isolation range depicted here. This probability can also be calculated more precisely with the formula $1/(1+e^{a+bX})$ (p. 767 in (Sokal & Rohlf, 1995)). A is the estimate for the intercept and b is the estimate for the variable, in this case -6.72 and 0.76 respectively. The RSquare value tells how much of the variation in presence-absence of *A.terrestris* that is explained by distance to the nearest mainland.

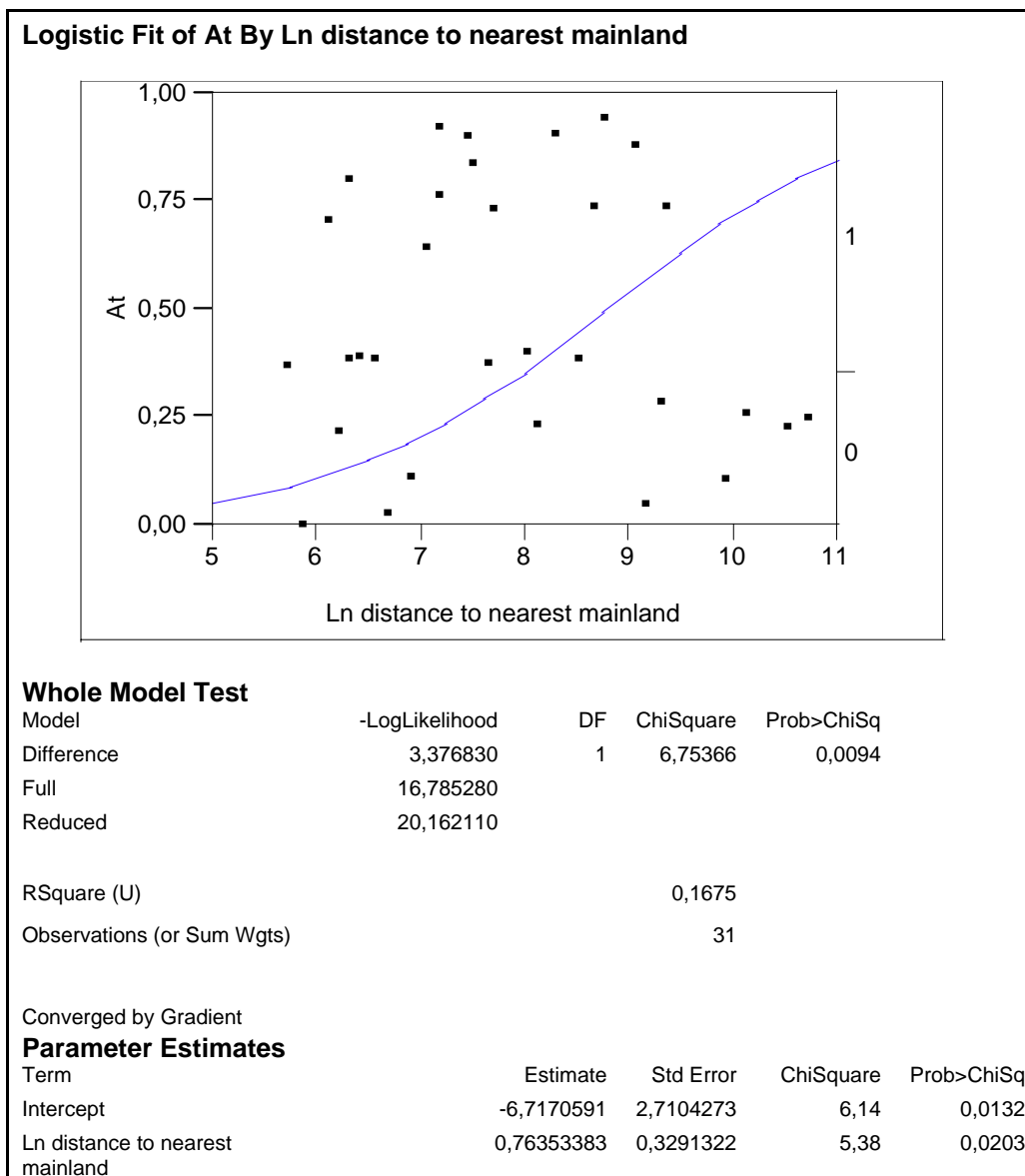


Figure 2. An example of the JMP (SAS, 2002) datasheet resulting from fitting (Y by X) a variable significant in explaining the presence-absence of a species on an island.

To test if there were any difference in the number of species between oceanic islands and landbridge islands when the variation stemming from island size and isolation have been removed, simple regression were carried out between these two factors and the total number of species and from this the residuals were saved. The residual values from the oceanic islands (Fanø, Læsø) were compared with the mean from the continental sample (see pp. 228 (Sokal & Rohlf, 1995)). The null hypothesis is that there is no difference. Egholm is not included in this test because of its close proximity to the mainland and the fact that it

becomes nearly connected with it, when the weather conditions are right (see appendix 3 for description of Egholm and the other islands).

To measure the degree of nestedness of the species presence absence matrix, the method proposed by Atmar and Patterson was used (Atmar & Patterson, 1993). The metric used is the “matrix temperature” T , which ranges from 0° for a perfectly nested matrix to 100° indicating complete disorder. The significance of the T -values was assessed by a Monte Carlo simulation using the “nestedness calculator” (Atmar & Patterson, 1995).

Where the presence of a predator species can be questioned it was excluded from the calculations. If I had not caught any specimen of a species of rodent or shrew from a particular island the credibility of the source decided whether the species was included in the data set or not.

Results

Islands

In table 1 is given demographic data on the islands. “Nearest mainland” includes apart from Jutland also the two large islands Zealand and Funen, since they are presumed large and diverse enough to act as mainland to the small mammals included in this study. To be sure that this is not a false assumption, correlation tests of number of species against distance are made for both the distance to nearest mainland and for the distance to Jutland or Germany.

The relationship between species richness and island area in ha is depicted in figure 3. The z value is the slope of the log-log curve and is equal to 0.039 (MacArthur & Wilson, 1967).

The full equation is $S=3.24*A^{0.039}$.

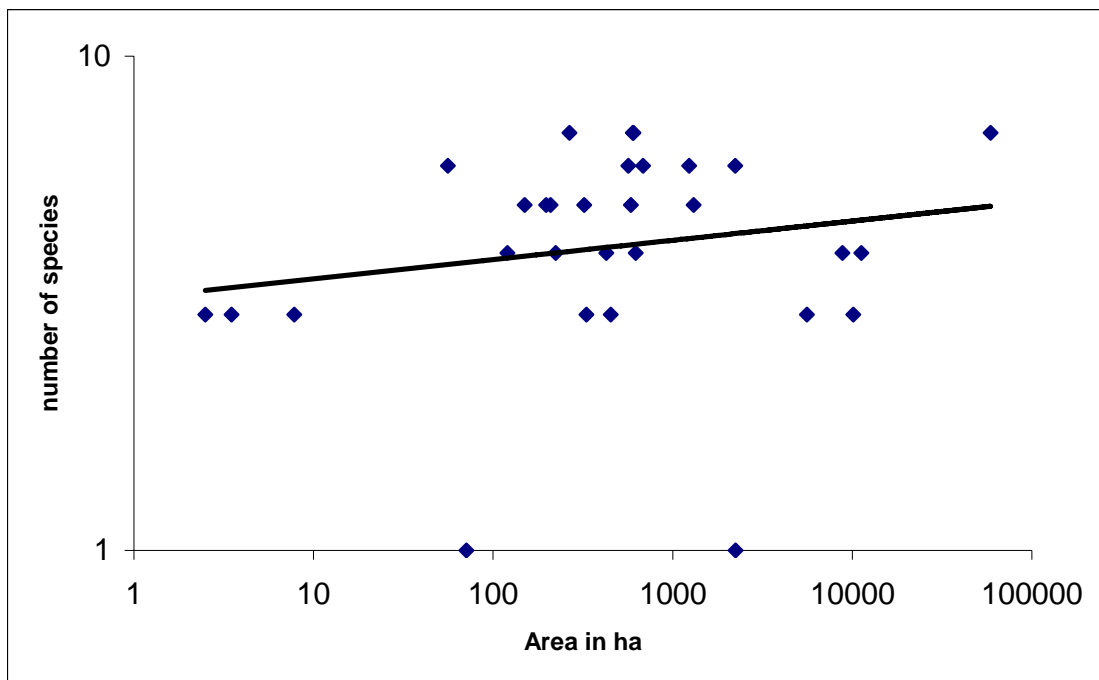


Figure 3. Species-Area log-log curve for small mammals on Danish islands. Equation: $S=3.24*A^{0.039}$. The logarithm used is the natural logarithm.

The Shannon ($H = -\sum P_i * \ln P_i$) and Simpson ($D = 1/\sum P_i^2$) diversity indices were calculated for each island and the results are given in table 2.

Table 2. Small mammal diversity indices for each island.

Island	Shannon index	Simpson Index	Island	Shannon index	Simpson Index
Agersø	1.410	2.88	Ll. okseø	0.719	1.89
Anholt	0.926	1.711	Lyø	1.369	2.518
Avernakø	1.502	2.983	Læsø	1.741	4.848
Barsø	1.367	2.645	Nexelø	1.715	4.616
Bjørnø	1.405	3.06	Omø	1.460	3.143
Bornholm	1.166	2.285	Samsø	1.367	2.507
Baagø	1.308	2.387	Sejerø	1.272	2.377
Drejø	1.487	3.286	Skarø	1.337	2.727
Egholm	1.122	1.988	St. Okseø	1.103	2.729
Endelave	1.580	3.558	Vigelsø	1.079	2.637
Fanø	1.975	5.958	Vorsø	1.162	2.621
Fur	1.628	3.485	Vorsø kalv	0.919	2.299
Hesselø	1.287	3.115	Æbelø	1.292	2.819
Hjarnø	1.015	1.904	Ærø	1.175	2.05
Hjelm	1.017	2.48	Årø	1.604	3.744
Livø	1.805	5.25			

The amount of cultivated land on each island had a clear effect on the Simpson Index but apparently very little effect on the Shannon Index. Figure 4 shows that when those islands without agriculture were excluded there was a clear negative relationship between the Simpson Index and the percentage of farmland. Those islands without farmland are often dominated by some other nature type, covering more than 50% of the land (appendix 1).

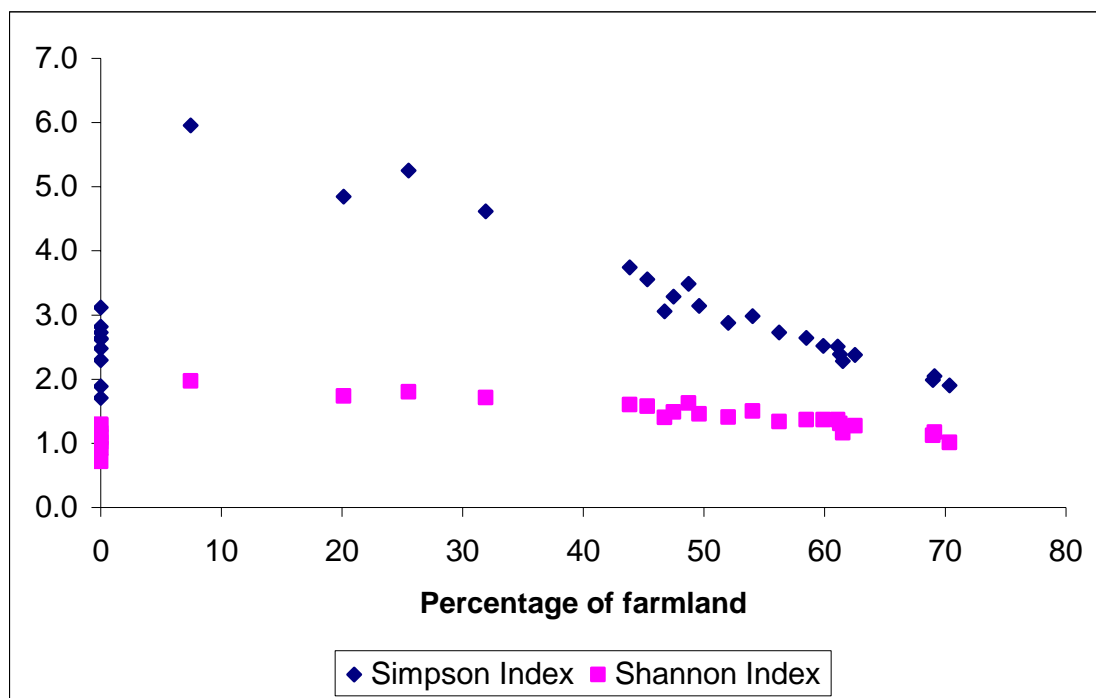


Figure 4. Effects of the amount of farmland on the Shannon Index and the Simpson Index.

To be able to perform parametric tests on the island data the following variables were tested for normality on a 5% basis: island size, distance, number of inhabitants and geological age. Number of habitats and two diversity indices were also tested and the results are given in table 3. The number of predator species on each island was not tested, but assumed normally distributed. This was because of the very narrow range, 1-5 predators per island.

Table 3. Tests for normality for island variables. Distributions marked with * means that the values were slightly higher than 5%. P values > 5% indicates that there is no deviation from normality

Variable	N	Transformation	Test	Distribution	Test Value	P
Island size	31	Ln	Shapiro-Wilkes	Normal	0.962	0.369
Distance to nearest mainland	31	Ln	Shapiro-Wilkes	Normal	0.95	0.188
Distance to Jutland/Germany	31	-	Kolmogorov-Smirnoff	LogNormal*	0.189	0.01
Number of inhabitants	31	Ln (x+1)	Shapiro-Wilkes	Normal	0.947	0.152
Geological age	31	-	K-Smirnoff	LogNormal*	0.301	0.01
Number of Habitats	31	-	K-Smirnoff	LogNormal*	0.272	0.01
Shannon Index	31	-	Shapiro-Wilkes	Normal	0.993	0.998
Simpson Index	31	Ln	Shapiro-Wilkes	Normal	0.951	0.195

The variables distance to Jutland/Germany, geological age and number of habitats have values slightly lower than 5% and were all tested with the non-parametric Spearman-rank correlation to make sure that this deviation from log-normality made no difference. In nearly all correlations between these three variables and the remaining ones, the use of non-parametric tests did not influence significance level. In two correlations there was a difference. These are number of habitats-distance to nearest mainland, where the pairwise test gave a close to significant result $P=0.055$ and the Spearman-rank a significant result $P=0.045$ and number of predators- distance to Jutland/Germany where the pairwise test gave a $P=0.042$ and Spearman-rank a $P=0.071$. These differences were regarded as minor and without importance to the general conclusions and parametric tests were used for the remaining statistical tests.

Mice

The immigration time for the species is given in table 4. For many of the species the presumed immigration times are some time before the first bone findings. Where this is the case it will be mentioned in the discussion.

Table 4. Immigration time and chronoperiod of the included rodents and shrews into Denmark. Data mostly from (Aaris-Sørensen, 1998)

Species	Immigration time (based on bone findings)
<i>Arvocola terrestris</i>	13.000-13.600 BC
<i>Sorex minutus</i>	13.000-13.600 BC
<i>Sorex araneus</i>	13.000-13.600 BC
<i>Apodemus flavicollis</i>	Boreal (8250-7000 BC)
<i>Clethrionomus glareolus</i>	Boreal (8250-7000 BC)
<i>Apodemus sylvaticus</i>	Atlantikum (from 7000-3800 BC)
<i>Microtus agrestis</i>	Atlantikum (from 7000-3800 BC)
<i>Neomys fodiens</i>	Atlantikum (from 7000-3800 BC)
<i>Mus musculus</i>	Early sub atlantikum (500 BC-present)
<i>Microtus arvalis</i>	Sub atlantikum (500 BC-present)
<i>Rattus norvegicus</i>	Around 1700 AD
<i>Micromys minutus</i>	1820 AD

Data on total number of species and number of species excluding *R.norvegicus* and *M.musculus* were tested for normality. Results are given in table 5. For reasons for excluding *M.musculus* and *R.norvegicus* see the analyses section in part one.

Table 5. Tests for normality of species data. Distributions marked with * were close to normal. Rn are *Rattus norvegicus* and Mmm are *Mus musculus*.

Parameter	N	Test	Distribution	Test Value	P
All species	31	Shapiro-Wilkes	Normal*	0.929	0.049
Number of species excl. Rn & Mmm	31	Shapiro-Wilkes	Normal	0.931	0.054

Catches

Not all species have actually been caught on the islands where they are reported in table 6. Some species are only reported from dead individuals brought home by domestic cats or individuals found dead in nature. Other species again have been reported from their presence in owl pellets or they have been heard, as for the shrews. Data from owl pellets were included where the islands are at some distance from the mainland. This is because owls rarely fly over water and would not normally do it between a meal and regurgitation (K. Dichmann, *pers. com.*).

The total number of species found on an island varied between zero and seven. This means that none of the included islands whatever their size or adjacency to the mainland have all species. On the 26 islands where trappings were done systematically after the method

described here 2485 individuals were caught on 8030 trap nights, which is 0.31 individual per trap night. For all data see table 6. The variation from island to island was very great, from close to zero to almost 1 per trap night. On Hesselø and Hjelm no trappings were done.

Table 6. Number of small mammals caught on each island. Where total number of specimens caught is not known or the species have been reported but not caught it is marked with x. Trap nights are number of traps times the number of nights they were left to stand.

Island	Month of trapping	Number of trap nights	Individuals per trap night	A.flavicolis	A.sylvaticus	A.terrestris	C.glaucolus	M.minutus	M.agrestis	M.arvalis	M.musculus	R.norvegicus	S.araneus	S.minutus	N.fodiens	Total
Agersø	032002			x		x		x	x		x				x	
Anholt	092001	340	0,24								82					82
Avernakø	102002	220	0,88		17		122				1		51		3	194
Barsø	012004	280	0,53		57	1	86	3			x	x	2			149
Bjørnø	102002	180	0,50		51	x		34			2				3	90
Bornholm	032003	420	0,19	13	38	x					x	x	24	3		78
Baagø	012004	280	0,14		26	2			11		x					39
Drejø	102003	220	0,66		104	x	40				1					145
Egholm	112003	280	0,38		51	x		12	17		x	x	25			105
Endelave	052004	420	0,08		34			x			x	x				34
Fanø	082003	280	0,06		13	x					4					17
Fur	082002			x		x			x		x	x	x			
Hesselø											x					
Hjarnø	012004	300	0,14	17				14	10		x	1				42
Hjelm																
Ll. Okseø	082004	160	0,92				144		1					2		147
Livø	052001				x	x					x					
Lyø	102002	430	0,16		13	x		1	16		9	x	30			69
Læsø	122002	340	0,49		165						2	x				167
Nixelø	082003	180	0,14		22	x			4		x					26
Omø	082003	200	0,28		51	1					4					56
Samsø	022003	360	0,06		21						x	x		2		23
Sejerø	082003	260	0,12		21	x	x		9		x	x				30
Skarø	102003	220	0,68		114	x					10	x	25			149
St. Okseø	082004	200	0,60				110		9							119
Vigelsø	072003	180	0,03			x			5			x	1			6
Vorsø	101984	561	0,61			x		305	26		1	x	10			342
Vorsø Kalv	101984	75	0,67			x		44	6							50
Æbelø	082000	1084	0,16		7			x	66		x			99		172
Ærø	012003	300	0,24		72	x					x	x				72
Årø	112003	260	0,32	17		x		20		8	x		31		6	82
Total for all islands		8030	0,31	47	877	4	502	433	180	8	116	1	201	104	12	2485

For each species the number of individuals caught per trap night is given in table 7. *Apodemus sylvaticus* and *M. minutus* are quite abundant and especially *C. glareolus* is very abundant on the islands where it occurs. *Mus musculus* was only caught in substantial amounts outdoors on Anholt. The number of individuals caught there amounts to 0.24 per trap night.

Table 7. Number of individuals caught per trap night for the eight species normally caught in the Ugglan traps. Numbers for each species are an average of the numbers for each of the islands where that species is caught.

Species	Individuals per trapnight
<i>Apodemus flavicollis</i>	0.051
<i>Apodemus sylvaticus</i>	0.185
<i>Micromys minutus</i>	0.187
<i>Microtus agrestis</i>	0.041
<i>Microtus arvalis</i>	0.031
<i>Clethrionomys glareolus</i>	0.499
<i>Sorex araneus</i>	0.072
<i>Sorex minutus</i>	0.035
<i>Neomys fodiens</i>	0.018

For each catch the habitat type was noted. These were categorised into six main habitat types, tree or bush covered, permanent grass areas, water bodies, moors and sand dunes, agricultural lands and buildings. For the species *A. flavicollis* (Af), *A. sylvaticus* (As), *C. glareolus* (Cg), *M. agrestis* (Mag), *M. minutus* (Mm) and *S. araneus* (Sa) the results are given in table 8. For the remaining species except *M. musculus* the catches were less than 20 and they were therefore not included. For *M. musculus* more than 2/3 of the specimens were caught on Anholt and since *M. musculus*' distribution on this island is very different from its normal distribution (Hansen et al., 2003) these specimens were not included.

Table 8. Catches distributed on the six main habitat types. Not all species were included due to lack of specimens.

Habitat type	Af	As	Cg	Mag	Mm	Sa
Tree cover	0.70	0.49	0.75	0.20	0.20	0.22
Grass cover	0.15	0.32	0.16	0.60	0.41	0.56
Lakes & streams	0.11	0.10	0.02	0.09	0.25	0.12
Moor & sand dunes	0.00	0.03	0.04	0.06	0.02	0.00
Farm land	0.04	0.06	0.02	0.02	0.04	0.09
Buildings	0.00	0.01	0.00	0.03	0.08	0.00
Total	1.00	1.01	0.99	1.00	1.00	0.99
Specimens in all	47	872	502	115	433	201

Part 1 – Species diversity

Analyses

Correlation tests for selected parameters are shown in table 9 (for all correlation test values see appendix 4). Size was significantly correlated to both Shannon Index ($P < 0.01$), number of habitats ($P < 0.0001$), number of predators ($P = 0.01$) and distance to mainland ($P < 0.001$).

Number of species was significantly correlated to number of habitats ($P < 0.014$) and number of predators ($P < 0.005$), and very close to significantly correlated to number of inhabitants ($P = 0.061$).

Table 9. Correlation between selected variables. Test used was parametric pairwise correlation analysis.

Variable	By variable	Correlation	N	P
Ln Size	Number of Species	0,274	31	0,135
Ln Distance to nearest mainland	Number of Species	-0,307	31	0,093
Distance to Jutland/Germany	Number of Species	-0,089	31	0,636
Geological age	Number of Species	0,003	31	0,987
Simpson index	Number of Species	-0,059	31	0,751
Shannon index	Number of Species	0,174	31	0,349
Number of Inhabitants	Number of Species	0,341	31	0,061
Number of Habitats	Number of Species	0,438	31	0,014
Number of Predators	Number of Species	0,495	31	<0,005
Ln Size	Number of Predators	0,448	31	0,012
Ln Size	Shannon Index	0,465	31	<0,01
Ln Size	Number of Habitats	0,814	31	<0,0001
Ln Size	Ln Distance to mainland	0,57	31	<0,001

Mus musculus and *R.norvegicus* are normally considered very closely connected to human activity. In most cases they are unable to survive and breed without the presence of humans (Hansen et al., 2003), (Jensen, 1982) and in other studies they have been excluded from the statistical analysis (Millien-Parra & Jaeger, 1999). A second set of correlation tests were therefore carried out to test whether their exclusion made any difference. The results are given in table 10. The exclusion of *M.musculus* and *R.norvegicus* made the correlation between distance and number of species significant ($P = 0.006$). Number of predators were still correlated with number of species ($P = 0.029$).

Table 10. Correlation between selected parameters. *Mus musculus* and *R. norvegicus* were excluded from total number of species. Test used was parametric pairwise correlation analysis.

Variable	By variable	Correlation	N	P
Ln Size	Number of Species (excl. Mmm and Rn)	0,032	31	0,864
Ln Distance to mainland	Number of Species (excl. Mmm and Rn)	-0,479	31	0,006
Distance to Jutland/Germany	Number of Species (excl. Mmm and Rn)	-0,105	31	0,574
Geological age	Number of Species (excl. Mmm and Rn)	0,079	31	0,675
Number of Predators	Number of Species (excl. Mmm and Rn)	0,393	31	0,029
Number of Inhabitants	Number of Species (excl. Mmm and Rn)	0,132	31	0,478
Number of Habitats	Number of Species (excl. Mmm and Rn)	0,264	31	0,151

Explanatory power of the nine included variables was estimated using multiple regression analysis for all species and with *R.norvegicus* and *M.musculus* excluded. Results are given in table 11 and 12. In both cases distance and the two diversity indices were found to have a significant influence on number of species. Distance and the Simpson index had a negative effect and the Shannon index a positive effect on species diversity.

Table 11. Multiple regression. Only significant variables included. All species included. N=31

Variable	Estimate	F	P	R ²
Intercept	5,1947			
Distance (Log transformed)	-0,6479	13,154	0,0012	
Simpson Index (Log transformed)	-9,8634	23,132	0,0001	
Shannon	10,9775	25,367	<0.0001	
				0,535

Table 12. Multiple regression. Only significant variables included. *R.norvegicus* & *M.musculus* excluded. N=31

Variable	Estimate	F	P	R ²
Intercept	5,7723			
Distance (Log transformed)	-0,6722	19,106	0,0002	
Simpson Index (Log transformed)	-6,3142	12,791	0,0013	
Shannon	6,9317	13,648	0,001	
				0,491

Bornholm is more than five times the size of the second largest island and its exclusion/inclusion in the analysis was found to have great effect on the explanatory power of the variables in the regression analysis. The results of the regression analyses with Bornholm excluded are given in table 13 and 14.

Table 13. Multiple regression. Only significant variables included. All species included. Bornholm excluded N=30

Variable	Estimate	F	P	R ²
Intercept	6,1514			
Distance (Log transformed)	-0,8649	32,274	<0.0001	
Simpson Index (Log transformed)	-9,8813	36,475	<0.0001	
Shannon	11,4352	43,067	<0.0001	
				0,695

Table 14. Multiple regression. Only significant variables included. *R.norvegicus* & *M.musculus* excluded. Bornholm excluded N=30

Variable	Estimate	F	P	R ²
Intercept	4,9735			
Size (Log transformed)	-0,3509	5,376	0,029	
Distance (Log transformed)	-0,6989	25,124	<0.0001	
Simpson Index (Log transformed)	-9,3171	25,918	<0.0001	
Shannon	11,5039	25,645	<0.0001	
				0,731

In all regression tests probability to enter was 0.1 and probability to leave 0.05. The same tests were run with probability to enter 0.25, but this made no difference in any of the four tests.

The comparison of species number on Fanø and Læsø to the other islands when the variation from island size and isolation was removed showed that both Fanø and Læsø have negative residual values and thus lies below the predicted number of species, when the variation from island size and isolation was removed. Fanø has a significantly poorer fauna ($t=2.698$, $P<0.02$, $df=28$) than the landbridge islands, but Læsø did not differ significantly ($t=1.106$, $P=0.2-0.4$, $df=28$). For all residual values see table 15. The mean residual value for all islands was 0.17 and the standard deviation was 1.33.

Table 15. Residual values for all islands from a multiple regression of number of species with island size and isolation.

Island	Residual value	Island	Residual value	Island	Residual value
Agersø	1,18	Fur	-0,65	Samsø	-0,94
Anholt	-1,77	Hesselø	-0,37	Sejerø	2,06
Avernakø	0,63	Hjarnø	-0,31	Skarø	0,69
Barsø	2,47	Hjelm	-2,81	St. Okseø	-0,66
Bjørnø	-0,01	Lille okseø	-0,53	Vigelso	-1,64
Bornholm	2,23	Livø	-0,88	Vorsø	1,33
Baago	-0,49	Lyø	2,20	Vorsø kalv	0,84
Drejø	0,40	Læsø	-1,32	Æbelø	0,13
Endelave	2,13	Nixelø	-0,78	Ærø	-0,76
Egholm	0,82	Omø	-0,74	Årø	1,03
Fanø	-3,47				

Discussion

Catches

In this study a total of 0.31 individuals of all species were caught per trap night. This is considerably more than Ursin (Ursin, 1948a) got in his study in the South Funen Archipelago. During 3900 trapnights he caught 400 individuals, i.e. 0.103 per trap night. The reason for this is probably that I conducted year round trapping, whereas Ursin only trapped animals during the summer from June to August, i.e. when the population densities for many species of small mammals are lowest (Ylönen et al., 1991), (Hoffmeyer & Hansson, 1974). If only the nine islands where trapping was done between May and August is included the mean of 0.31 is reduced to 0.20. Of these Store Okseø and Lille Okseø seem to deviate from the norm with 0.60 and 0.92 individuals per trap night, and if they are excluded the mean is 0.13 per trap night. No matter whether St. Okseø and Ll. Okseø are included or not it seems that year round trapping increases the overall catch. The apparently very high population densities on St. Okseø and Ll. Okseø are most likely a result of their small sizes and the lack of mammal predators. Populations of rodents on islands often exhibit a higher average density than those on the mainland because of the lower emigration possibilities, and the smaller the island the stronger is this relationship (Adler & Levins, 1994).

The higher number of catches experienced in this study could also be caused by changes in trappability of the small mammals during the year, i.e. that the responses of rodents towards the traps change with the season. Kikkawa found that trappability increased in late autumn and winter (Kikkawa, 1964), but Hansson (Hansson, 1967) claims that this effect is caused by migration. *A.sylvaticus* migrates from open fields into the forest after harvest, which is where Kikkawa did his trappings in autumn. My trapping was done in a mixture of habitat types though, and therefore any seasonal migrations from one habitat type to another probably would not affect the overall catches per trap night.

The numbers reported here of total catches are subject to a certain amount of uncertainty and should not be taken as a precise estimate of the population densities. The possible changes in trappability reported by Kikkawa (1964) will affect the number of individuals sampled from the same population. The number of traps used and the spacing between them will also affect the size of the catch. The more traps used the larger the catch until an

asymptote is reached (Tew et al., 1994) and though Ursin (Ursin, 1948a) used about the same trap spacing as I did, he did not state the total number of traps used on each island.

Island size effects

According to MacArthur and Wilson's Island Biogeography theory the number of species at equilibrium varies with the size and the isolation of an island (MacArthur & Wilson, 1967). They do not however give any explanations as to which of these factors have the greatest influence on the total species number within different taxa. In a study of terrestrial vertebrates in Georgian Bay Islands National Park, North Eastern USA, Schmiegelow and Nudds (1987) found that island size accounted for about 70% of the variation in the number of species. This value was consistent for all included groups, i.e. birds, reptiles, amphibians and nonvolant mammals (Schmiegelow & Nudds, 1987). They do not specify which species are included though. Yom-Tov et al. (1999) also found that island area can explain more than 70% of the variation in species number in their studies of rats and mice in New Zealand. These results are not confirmed by the results in this study, where island size is found to have no explanatory effect on the number of species when multiple regression analysis is carried out ($P=0.29$ and $P=0.76$ if *R. norvegicus* & *M. musculus* are excluded). This lack of correlation between number of species and island area is not consistent with the results of Grant (1970). He compared three archipelagos in Denmark, UK and Canada and found that the Danish islands were actually the only ones with a significant correlation between area and species. He also stated that, in accordance with MacArthur and Wilson's equilibrium theory (1967) the importance of area diminished with isolation of the island. This might be the reason why he found significant area-species correlations in Denmark in contrast with the other archipelagos in his study and in contrast with the results of this study. The data used by Grant are from Ursin (1950) and these data did not cover all the Danish isles, only the south Funen archipelago and these islands are mostly within a few km from the mainland. If all the Danish islands are considered much more variation in the distance to the mainland is encountered. This would make the Danish data much more like the data from the other two archipelagos investigated and then his results might also have been more consistent with the ones found in this study.

Only in one part of the analysis did size come out as significant. If Bornholm, *R.norvegicus* and *M.musculus* were excluded then the island size relationship became significant ($P=0.029$). The reason for this is probably that Bornholm is more than five times the size of the second largest island but do not have a correspondingly larger number of species. This deviation might have a distinct effect on the slope of the regression line.

The lack of size effects in this study might thus be a result of the large variation in island size created by the inclusion of Bornholm. Island size is significantly correlated with the diversity measures: the Shannon index ($P<0.01$) and number of habitats ($P<0.0001$), but these measures have much less variation and therefore they will come out as significant in a multiple regression analysis.

The large variation in island size caused by the inclusion of Bornholm and the accompanying effect on the slope of the regression line is also the most likely explanation as to why the explanatory power of the variables in the regression analyses increases ca. 20% when Bornholm is excluded. This happens in spite of the fact that it is the exact same variables that are significant in explaining the number of species.

Habitat diversity effects

The theoretical value of the z parameter, i.e. the slope of the log-log species-area curve in the theory of island biogeography is 0.26-0.27 (MacArthur & Wilson, 1967), (Preston, 1962a), (Preston, 1962b). When very large islands are included this value can be higher than the predicted one. This results from the fact that when islands become larger their topography becomes more complex and the habitats more heterogeneous. This creates a number of “pseudo” islands that support a larger species accumulation than a more homogeneous island. According to MacArthur and Wilson (1967) the diversity of an island should thus be very much correlated with its size. That prediction is confirmed by two of the three diversity measures applied in this study. Number of habitats and the Shannon index were both significantly correlated with island size ($P<0.0001$ and $P<0.01$ respectively). The Simpson index however showed no correlation with island size. This might be because the Simpson index is only sensitive to the abundance of the more dominant habitat types and is best regarded as a measure of dominance concentration (Hill, 1973). The Simpson index estimates the probabilities of picking two habitat type samples at random that are of different types (Danoff-Burg, 2000). This means that the more dominated an island is by a

particular habitat type the lower the Simpson index value becomes, and in this study islands dominated by a single nature type are not only small ones. On the contrary, large islands like Anholt and Ærø have 75% moors and 70% agricultural land respectively and thus the correlation between islands size and the Simpson index disappears ($P=0.317$).

The Simpson index does however come out as a significant variable in the multiple regression analyses, but with a negative effect on the number of species. One reason for this might be the correlation between the proportion of a dominant nature type and the Simpson index values. Farmland is dominating many islands and cultivated land harbours fewer species of small mammals than uncultivated areas (Jensen & Hansen, 2003). This negative relationship between the amount of cultivated land and the Simpson index is very likely also the reason that the two positively correlated variables, the Shannon index and the Simpson index have opposite effects on the number of species. The Shannon index shows no correlation with the amount of farmland and is thus not affected by the negative effect of agriculture on the number of small mammal species.

In this study I show that a nature type does not have to be present in very large quantities to allow the presence of a species dependent upon it. *Neomys fodiens* has long been known to be associated with the presence of water bodies (Carlsen, 1995), (Winge, 1908), but in this study it was found on islands where water covered $\leq 1-4\%$ of the land.

When calculating the Shannon index the logarithm of the presence of each nature type is taken ($H = -\sum P_i \cdot \ln P_i$). Using logarithms emphasizes the relative importance of rare events and reduces the relative effects of common events (Fano, 1961 cited in (Atmar & Patterson, 1993)). By stressing the importance of the less abundant nature types I therefore argue that the Shannon Index gives a better picture of an island's suitability for small mammals than the Simpson index.

Isolation effects

Many of the studies already mentioned in this report find no isolation effects (see for example (Millien-Parra & Jaeger, 1999), (Brown, 1971)). In a review article only 10 of 18 archipelagos inhabited by non-volant mammals were found to exhibit a significant relation between number of species and isolation (Lomolino, 1984). Like Grant (1970) Lomolino

included Ursin's data from the South Funen Archipelago (Ursin, 1950) and they both found that these data showed a significant relationship between an island's isolation and its species number. That is in accordance with the results of this study where the distance to the mainland and the number of species were close to being significantly negatively correlated ($P=0.093$). When *R.norvegicus* and *M.musculus* are excluded the negative correlation between island isolation and number of species become significant ($P=0.006$). This is probably because these two species are the ones most closely connected with human activities. Their immigration to Denmark was facilitated by human activities (Aaris-Sørensen, 1998) and it is probably safe to assume that their dispersal to the islands took place in the same way. Subsequently they are not expected to be affected by distance and their exclusion makes the relationship between number of small mammals and isolation more clear. Lomolino (1984) found that Murid rodents (*Muridae*) have very poor species-isolation correlations and relatively high z-values for mammals. He correlates this with their dependence on anthropogenic immigrations. He also judges that the Murid's immigration rates are more likely to be correlated with island size than isolation. This conclusion originates from a study in the Malay Archipelago, but does not seem to be generally applicable. His findings are certainly not consistent with the ones found in this study, where all the included rodents are Murids.

The lack of isolation effects reported in many studies could be artefacts of the choice of archipelago. It has been suggested that the apparent unimportance of isolation is due to the rather narrow range in isolation values used in those studies (Lomolino, 1982). Lomolino (1982) states that the ranges of isolation studied are often unsuitable for the poor immigration abilities of terrestrial mammals and that the small differences in distances to the mainland between islands in very distant archipelagos make no difference in immigration rates and subsequently in equilibrium numbers of species (Lomolino, 1984), (Lomolino, 1982).

The isolation values used in this study range from almost connected to the mainland at low tide and certain wind directions (Vorsø and Egholm), i.e. no isolation, to very isolated 45 km off the nearest coast. They seem quite appropriate for studying small terrestrial mammals and they more or less match those of Adler and Wilson (1985) who found significant isolation effects for several species of small mammals, including species of the genera *Sorex*

and *Clethrionomys*. The appropriateness of the isolation values used in this study is also confirmed by reports of newly immigrated mammals to some islands. If the islands were so isolated that no isolation effects were apparent, no immigration events would be possible at all unless by human intervention. *Clethrionomys glareolus* is reported new to both Drejø and Sejerø by local residents (within the last 8-10 years) and *R.norvegicus* has recently established itself on Barsø. *Rattus norvegicus* could easily have been transported to the island with humans, but is also a very able swimmer (Winge, 1908) and should be able to cross the 1700 m gap between Barsø and the mainland either in summer or winter. *Clethrionomys glareolus* is not very closely connected with humans and it is feasible that it has colonised at least Drejø without the help of humans, since it is a fairly good swimmer and contrary to expectation an effective coloniser of experimentally cleared woodlots (Ursin, 1950), (Ylönen et al., 1991).

Not only the distance to the nearest mainland has a significant role in determining the isolation of an island, but also the distance to the nearest other island. According to MacArthur and Wilson's theory (1967) stepping stones contribute to the exchange of species between source areas and the less able the disperser the more important the role of the stepping stones. Accordingly it should be very important to the rodents and insectivores studied here, but most of the islands included here are closer to the mainland than they are to other islands. Thus it makes no sense to try and discern the contribution from "island hopping" mammals. Only south of Funen the islands are many and close enough to form a regular archipelago, but even there the data are not optimal for testing the steppingstone theory, since many of the islands lie in a more or less straight line along the South Funen coast. The data collected in this study does however provide two examples of apparent stepping stone immigration.

The two large islands Ærø and Samsø are of about the same size and have the same distance to the mainland. Samsø has only one stepping stone, whereas Ærø has many in the South Funen Archipelago. Still they have exactly the same number of species, but not the same composition of species. *Arvicola terrestris* is present on Ærø but not on Samsø. It is an excellent swimmer and its apparent favourite mode of immigration is swimming (Ursin, 1952b). *Arvicola terrestris* is very abundant on many small islands including those in the South Funen archipelago, and Ursin (1952) states that an island is more likely to become inhabited if it is situated in the vicinity of an overpopulated isle than near the mainland where

A. terrestris is not particularly common. Thus it is quite feasible that *A. terrestris* has immigrated to Ærø by stepping stones. Another example is *C. glareolus* on Drejø. According to the Drejø residents it has immigrated to the island 8-10 years ago. *Clethrionomys glareolus* is not present on very many of the smaller islands but is very abundant on Avernakø, which is the island closest to Drejø. The most probable entryway to Drejø for *C. glareolus* is thus via the stepping stone Avernakø.

Before the beginning of this study the assumption was that the two islands Funen and Zealand (3000 km² & 7000 km² approx.) were large and diverse enough to be considered mainland to the small mammals. Contrary to the large herbivores and the predators there have been no known extinctions of rodents and insectivores on these islands since the transition around 8000 years ago from one large landmass to archipelago (Aaris-Sørensen, 1998). The results support this assumption. There is no correlation between the total number of species and the distance to Jutland/ Germany (P=0.64) and this parameter never comes out as significant in any of the multiple regression tests. The conclusion is that the assumption was correct and this is supported by Lomolino's review (1984) where he also defines isolation as the distance to nearest mainland or nearest large island. He does not specify how large an island has to be to be considered large enough though.

Equilibrium vs. non-equilibrium fauna

In the literature there has been much discussion of how to define when a population is in equilibrium according to MacArthur and Wilson's theory (1967). Grant (1970) judges island assemblages to be in equilibrium if the species number is correlated with island area or isolation. Hanski (1986) on the other hand does not find that a species-area relationship proves the equilibrium theory. Other writers have suggested that if the z-value of the equilibrium equation ($S=c \cdot A^z$) is $z=0.26$ then the population is in equilibrium (Adler & Wilson, 1985), (Lomolino, 1982) and z values deviating much from this as evidence for disequilibrium (Brown, 1971). Though also this practise has been questioned ((Schoener, 1976) cited in (Adler & Wilson, 1985)) it seems to be the most widely used.

MacArthur and Wilson (1967) suggested that mammal communities may often depart from equilibrium due to their low immigration rates. Brown (1971) finds in his studies of

mammals a very high z value and he also attributes this disequilibrium to the low immigration rates of these. Brown (1971) also gives examples of other mammal assemblages that he does not believe to be in equilibrium for the same reason.

The very low z value of 0.039 found in this study is not in accordance with Brown's results, on the contrary. Preston (1962 a,b) writes that the less isolated an island is, the smaller the z value because of the larger immigration rates. This fits well with the fact that the average distance to the mainland of the islands included here is relatively low compared to many other studies (Lomolino, 1984). This low degree of isolation and the resulting higher immigration points to a non-equilibrium fauna, but is not conclusive. In a study similar to this Adler and Wilson (1985) also found a very low z -value of 0.06, but made no conclusions either as to the equilibrium state of the archipelago.

Another fact that points towards a non-equilibrium fauna is the time elapsed since the islands in the Danish archipelago were isolated. Case and Cody (1987) showed in their study in the Sea of Cortez that a period of 10.000 years was not enough to erase the differences in fauna richness between oceanic and landbridge islands and creates an equilibrium for the mammal fauna, even though it may be long enough for plants and land birds. Most of the Danish islands are younger than 10.000 years so they should not have attained equilibrium yet according to Case and Cody (1987).

When the differences in number of species between the two oceanic islands and the landbridge islands were tested only Fanø showed significantly fewer species ($P < 0.02$). Læsø has negative residual values when the variation from island size and isolation has been removed, but it is not statistically significant. Again the facts point towards non-equilibrium but are not conclusive.

A third circumstance supporting the notion that the Danish Archipelago is not in equilibrium as a whole is the idea that large islands are also often the more isolated ones. This could be from natural causes (Hanski, 1986) or like in Denmark from the entrepreneurship of man, building bridges and embankments to the large islands close to the mainland coast, thus changing them from islands to a form of peninsula. Therefore there are no large islands in Denmark which are not also very isolated, when those connected to the mainland by bridge or embankment are excluded. Crowell (1973) suggests that low

extinction rates on large landbridge/ continental islands allow an over-saturation with species. At the same time the immigration to more isolated islands depends on rare events and he proposes that the maximum limit to mammal dispersal is 25 km (Crowell, 1973). Thus according to Crowell large isolated islands like Bornholm should not be in equilibrium between immigration and extinction, but over saturated with species. This fits well with the fact that Bornholm has a large positive residual value when the variation from both size and isolation has been removed.

According to Yalden (1982) the mammal fauna of the British Isles cannot be explained by a simple recolonisation after the retreat of the ice, the process was much more complicated and accidental human introductions played a part. The same thing seems to be the case in the Danish archipelago. No single variable or theory can explain the composition of the fauna on the Danish islands. Under such circumstances each species and island has to be considered separately (Yalden, 1982). I will do this in the next section.

Part 2 – Individual species

Analyses

The degree of nestedness was tested for the two sets of data, first with all species included and next where *R.norvegicus* and *M.musculus* were excluded. The results are given in figure 5. Both data sets were significantly nested since the probability to get a more nested dataset by coincidence for 12 species was $P=5.5e-08$ and for 10 species $P=1.36e-03$. The simulations were run 500 times.

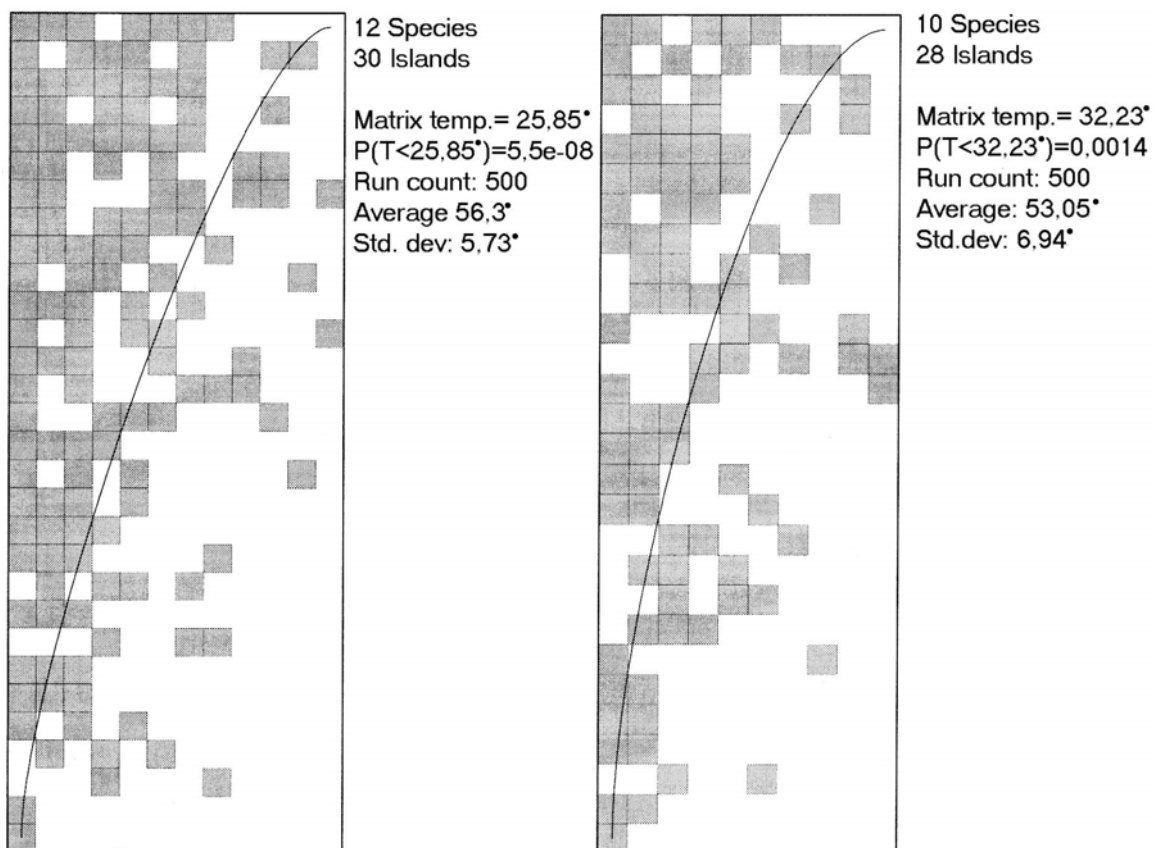


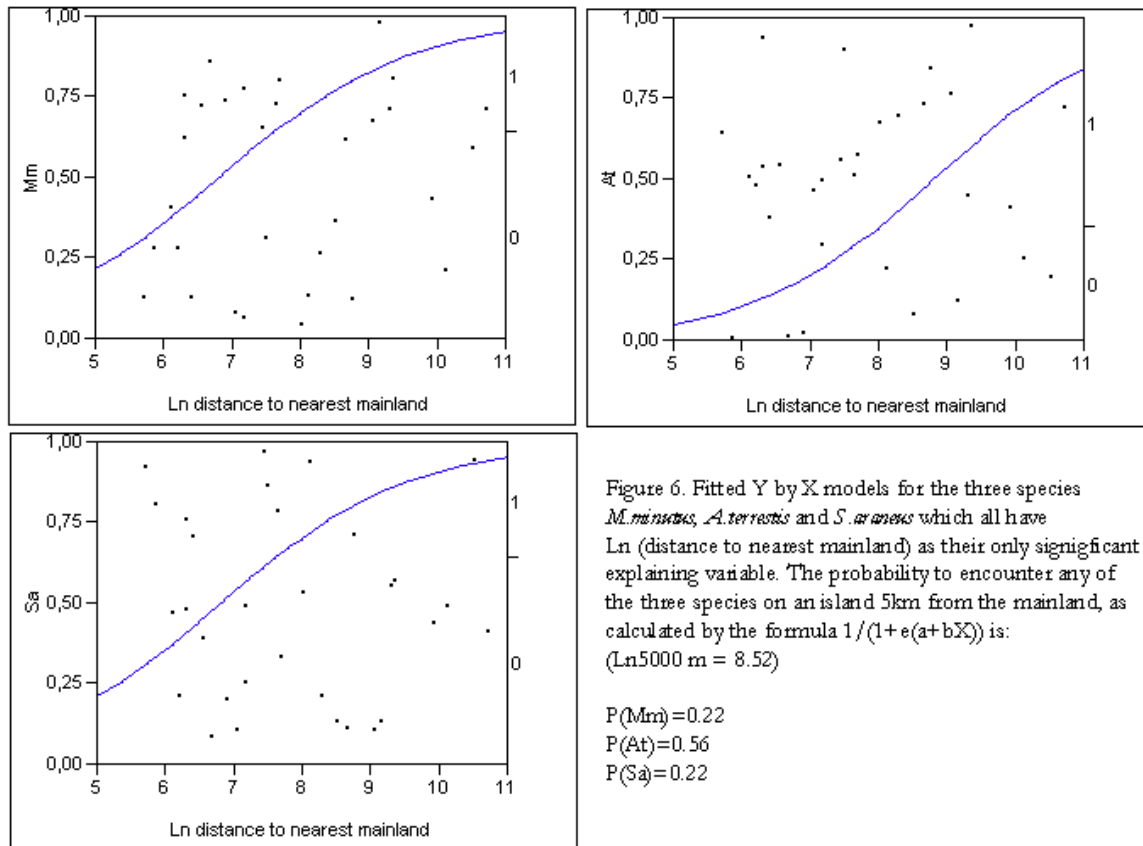
Figure 5. Nestedness for the two sets of data. All species included or *R.norvegicus* & *M.musculus* excluded. For method used see (Atmar & Patterson, 1995).

Then all species were tested to find variables significant in explaining the variation in the presence-absence of each species on each island. For all species except four these variables are given in table 16. For the species *C.glareolus*, *M.arvalis*, *N.fodiens* and *S.minutus* none of the included variables had significant explaining power.

Table 16. Variables that are significant in explaining the presence-absence of each species on the islands.

Species	Variable	Estimate	P	R ²
A.flavicollis	Ln (Nearest mainland)	1,372	0,046	0,391
	Ln (Number of inhabitants +1)	-0,953	0,022	
A.terrestis	Ln (Nearest mainland)	0,764	0,020	0,168
A.sylvaticus	Shannon Index	-15,871	0,013	0,366
	Ln (Simpson Index)	10,554	0,041	
M.agrestis	Ln (Nearest mainland)	1,619	0,008	0,527
	Simpson Index	5,671	0,047	
	Geological age	-0,001	0,034	
M.minutus	Ln (Nearest mainland)	0,718	0,040	0,135
M.musculus	Shannon Index	-12,690	0,029	0,526
R.norvegicus	Ln (Island size)	-0,499	0,038	0,146
S.araneus	Ln (Nearest mainland)	0,729	0,038	0,138

Next the significant variables were tested in a fit Y by X model and the graphic results of these tests are given in figure 6-11. The precise probability to encounter each of the species on an island as estimated from the significant variables can be calculated with the formula given in the methods section (p.767 in (Sokal & Rohlf, 1995)).



For an island situated 5km from the mainland the probability to encounter *M.minutus*, *A.terrestris* and *S.araneus* is 0.22, 0.56 and 0.22 respectively.

The two species most closely connected with human activity have one significant variable each. For *M.musculus* the probability of an encounter on an island with average diversity, i.e. with a Shannon Index value of 1.33 are $P=0.98$. For *R.norvegicus* the probability to encounter on an island of 1000 ha is $P=0.55$.

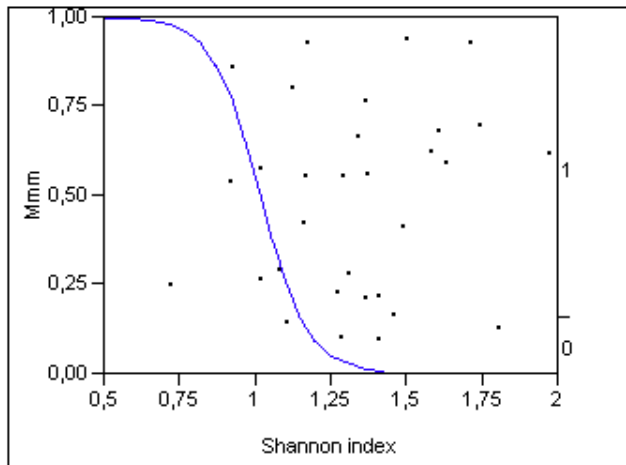


Figure 7. Fitted Y by X model for *M.musculus* for which the Shannon index is the only significant explaining variable. The probability to encounter *M.musculus* on an island with average diversity (Shannon index = 1.33) is:

$P=0.98$

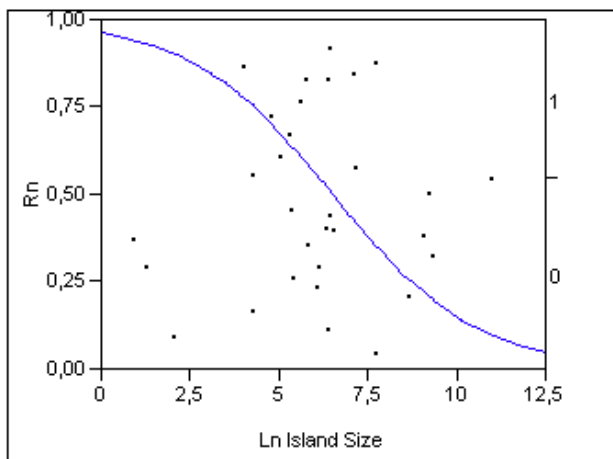


Figure 8. Fitted Y by X model for *R.norvegicus* for which Ln (Island size) is the only significant explaining variable. The probability to encounter *R.norvegicus* on an island of 1000 ha is: (Ln1000=6.91)

$P=0.55$

The field vole (*M.agrestis*) has three significant explaining variables, which together account for 52.7 percent of the variation in presence-absence of *M.agrestis*. The Simpson index and the distance to nearest mainland have a negative effect on the chance of presence of *M.agrestis*. The mean value of the Simpson index is 2.98 and on an island with this diversity there is 44% chance of encountering *M.agrestis*. For an island 5km off the mainland there is

33% chance of encountering *M.agrestis*. The age of an island has a positive effect on the presence of *M.agrestis* and for an 8000 year old island the probability is 64%.

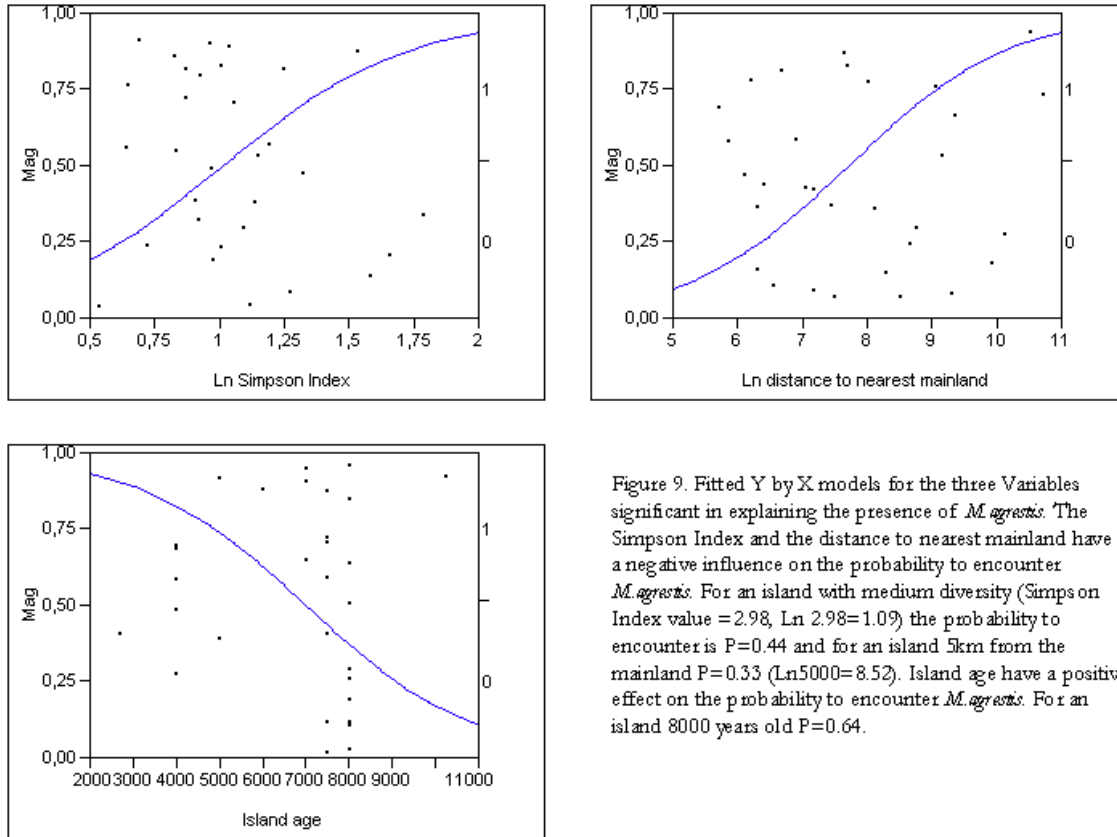


Figure 9. Fitted Y by X models for the three Variables significant in explaining the presence of *M. agrestis*. The Simpson Index and the distance to nearest mainland have a negative influence on the probability to encounter *M. agrestis*. For an island with medium diversity (Simpson Index value = 2.98, Ln 2.98=1.09) the probability to encounter is P=0.44 and for an island 5km from the mainland P=0.33 (Ln5000=8.52). Island age have a positive effect on the probability to encounter *M. agrestis*. For an island 8000 years old P=0.64.

The yellow-necked mouse has two significant variables, which together explain 39.1% of the variation in presence-absence of this species. The number of inhabitants has a positive effect on the presence of *A.flavicollis* and if an island with 500 inhabitants is considered, the chance of encountering this species is 23%. The isolation of an island has a negative effect and the probability to encounter *A.flavicollis* on an island 5km from the mainland is 14%. A caution should be taken though when interpreting the results for this species, since it is only present on 5 islands.

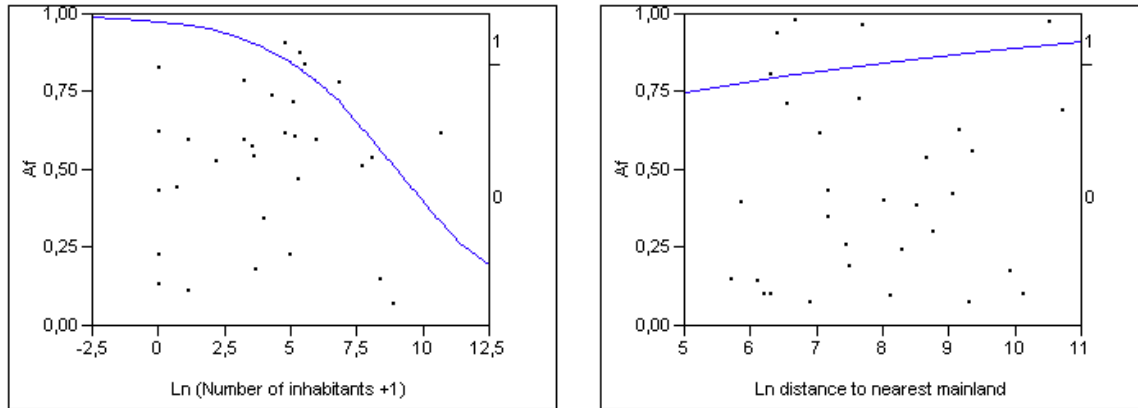


Figure 10. Fitted Y by X model of the two variables that have significant explaining power of the presence-absence of *A. flavicollis*. Number of inhabitants have positive effect on the presence of *A. flavicollis* and for an island with 500 inhabitants the probability of encountering *A. flavicollis* is $P=0.23$. Isolation has a negative but not statistically significant effect on the presence of *A. flavicollis*, and for an island situated 5km from the mainland the probability of encountering *A. flavicollis* is $P=0.14$.

The wood mouse (*Apodemus sylvaticus*) has two significant variables, which together explain 36.6 percent of the variation in presence-absence of this species. The two variables the Shannon and the Simpson index are however highly positively correlated ($r=0.91$, $P<0.0001$) and the result of this is that when each variable is fitted Y by X then the Simpson index does not have significant explaining power over the presence-absence of *A. sylvaticus* anymore ($P=0.12$). The Shannon Index still have a significant positive effect on the presence of *A. sylvaticus*.

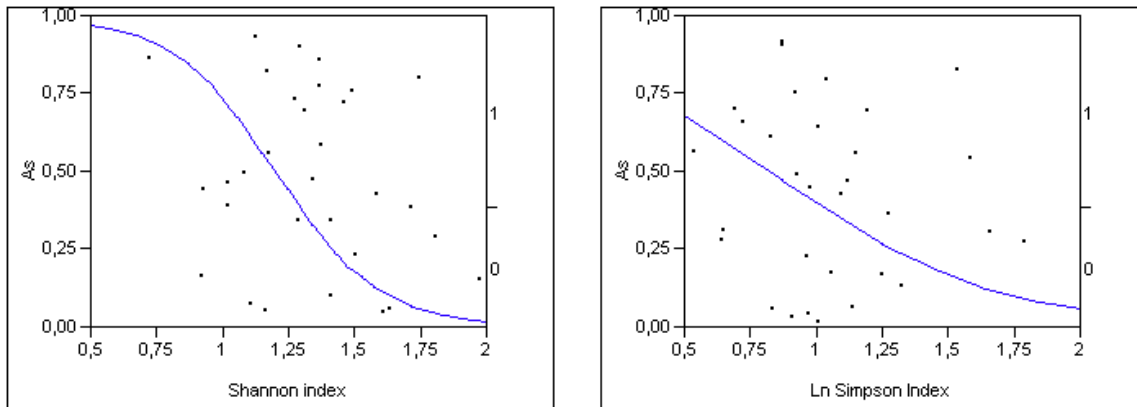


Figure 11. Fitted Y by X model for the two variables significant in the logistic regression test for *Apodemus sylvaticus*. Both the Shannon index and the Simpson index have a positive effect on the possibility of encountering *A. sylvaticus* but when fitted alone the Simpson index do not have significant explaining power ($P=0.12$). The probability to encounter *A. sylvaticus* on an island of average diversity (Shannon index = 1.33) is: $P=.065$.

Discussion

Nestedness

If island biotas were randomly drawn from the mainland species pool, then the islands of an archipelago should exhibit a species composition according to a random model, but examples of deviations from randomness on islands have long been known. One of these is the nested distribution (Darlington, 1957). This model describes a situation where a group of species on a small island will be a subset of those on the large islands, which because of their size have a larger overall species assembly. The nestedness model thus seems perfect for and is much used in presence-absence studies on islands (Atmar & Patterson, 1993).

There are two schools of thought when it comes to explaining why nested patterns arise on islands. Atmar and Patterson (1993) stressed the importance of extinction. They claimed that on each island in an archipelago according to its size there will always be one species closest to its minimum sustainable population size, and thus in greatest risk of local extinction. A line of islands going from large till small will therefore exhibit a very predictable extinction sequence. Other researchers stresses the importance of a differential dispersal and colonisation ability in the species in creating the nested patterns (Laázaro et al.).

The tests for degree of nestedness showed that the species in this study are distributed in a non-random fashion, that the species assemblies on each island are in fact nested. The Danish archipelago consists mainly of islands isolated by rising seas. Extinctions should therefore in theory have taken place and one example is given by Ursin ((Ursin, 1948b) who reports *M.agrestis* on Bjørnø in 1948. In 2002 it was not there anymore. On the other hand are the examples of newly immigrated species and the fact that *M.agrestis* is positively affected by island age and the probability of encountering it thus rises with the age of an island. Therefore immigration must play a role in the distribution patterns of at least *M.agrestis* if not all species.

Field vole (*Microtus agrestis*)

Microtus agrestis is one of the most abundant mammals in Denmark and common also on islands (Muus, 1993), (Manniche, 1935). In this study it has been reported on 15 of the 31 islands. Late immigration of the species cannot be held responsible for the absence on half

the islands. There are bone findings as old as 7500 years (Aaris-Sørensen & Andreassen, 1992) and it is presumed immigrated as early as the pre boreal period (10.000+ years ago) From one area it is conspicuously missing. Only one of the six islands in the South Funen Archipelago houses *M.agrestis*. At first look there seems to be no obvious reason for this since they are close to the mainland and have diversity indices around the mean. The mean values for the two significant variables the Simpson index and the distance to nearest mainland are for the south Funen islands are 2.8 and 4300 m. This gives a statistical probability for presence of *M.agrestis* of 50% and 35% respectively. This difference between expected and experienced presence might be entirely due to coincidence, but Ursin (1948b) also notes that its absence from most of the South Funen islands is conspicuous. One reason for its absence might be that these islands are among the youngest in the Danish archipelago. Island age comes out in the logistic regression as a positive factor for the presence of *M.agrestis*. The fact that the only island in the south Funen archipelago where it does occur is Lyø, which is isolated around 2000 years before the others seems to support this theory. Another reason for its absence might be the distribution of the different habitat types. *Microtus agrestis* is found on many types of habitat, but is known for its preference for permanent grassland with good vegetation cover and areas with young forest (Winge, 1908). That is in accordance with the findings in this study, where 60% of *M.agrestis* was caught on permanent grassland and 20% under tree cover. Most of the South Funen islands have little permanent grassland, below the mean for all the islands and are thus less suited for *M.agrestis* than islands with more grassland. The one island that has a substantial amount of grassland is Bjørnø, which formerly has also housed *M.agrestis* (Ursin, 1948b) even though it was not found there in 2002. In 1948 Ursin reported that *M.agrestis* was new to Bjørnø immigrated possibly over the ice in winter. So even though he also claims that *M.agrestis* is very short ranged and a poor disperser (Ursin, 1952b) it seems able to emigrate from the mainland to at least the less isolated islands, possibly by swimming since Manniche (1935) claims that it is a very able swimmer. Bjørnø is a small island though and *M.agrestis*' propensity for great population fluctuations (Jensen, 1993) could easily have caused its extinction on this island.

Common vole (*Microtus arvalis*)

Microtus arvalis is only present on two of the investigated islands. That is all likely because of its late immigration into Denmark. It was not registered here before the early sub-atlantic

period around 2000-2500 years ago, long after the isolation of the islands (Aaris-Sørensen, 1998). The two islands where it has been caught are the Jutland islands of Årø and Endelave and it has never been recorded in the literature on Funen, Zealand or north of Limfjorden. This indicates that it is not easily transported around with humans although it is presumed immigrated with the emergence of the open cultural landscape caused by the spreading of agriculture (Aaris-Sørensen, 1998).

Bank vole (*Clethrionomys glareolus*)

Clethrionomys glareolus immigrated to Denmark before the isolation of the islands (Aaris-Sørensen, 1998) but is now only present on 6 of the 31 islands. This very restricted island distribution is most likely the reason why none of the variables are significant in predicting the presence-absence of *C.glareolus*.

The distribution of the specimens caught here fits well with the general distribution of the species according to the literature (Winge, 1908), (Butet & Paillat, 1999). 75% have been caught in forest or tree covered small biotopes like hedgerows. Of the 16% caught in permanent grass most have been caught within 10-20 m of hedgerows or other tree covered biotopes. This is consistent with the results obtained by Hansen (Hansen, 1997) where *C.glareolus* is often caught in crops in late summer, but rarely more than 25 m from a hedgerow.

This pronounced preference for tree-covered biotopes does however not restrict *C.glareolus* to islands with large amounts of tree cover. Four of the six islands where it is present have considerably less tree cover than the mean for all the included islands (from 7-11%, mean for all islands is 17.3%). Thus *C.glareolus* makes a good example of the notion that a habitat type does not have to be present in large quantities to support the presence of a species dependent on it.

Clethrionomys glareolus has the highest density of all the included species, as measured by the catches per trap night. As mentioned above this cannot be the result of the presence of large amounts of its favourite habitat, since this is not the case in most of the islands where it is present. One thing that might contribute to this high density though is the fact that populations on islands often have a higher density than open populations on the mainland and that this relationship is strengthened the smaller the island. All of the islands where *C.glareolus* has been caught are less than 600 ha large and the island with the by far most

dense population of *C.glareolus* is also the smallest (Ll. Okseø). The fact that on most of the islands where *C.glareolus* have been caught the trapping has been done in the early fall might also contribute to high catches. This is the period where *C.glareolus* normally peaks in population density (Ylönen et al., 1991)

Water vole (*Arvicola terrestris*)

Arvicola terrestris was an early immigrant to Denmark and was present here at least 13.000 years ago, long before any of the islands were isolated (Aaris-Sørensen, 1998). It is still present on 19 of the 31 islands included. *A.terrestris* lives much of its life underground and is rarely caught in the traps used in this study. Therefore a discussion of its habitat preferences or population densities will not be attempted here. Its population densities are very high on many small islands though (*pers. obs.*), (Muus, 1993) and according to Muus (1993) this is because of the lack of predators on the small islands. I have not found any significant relationship between number of predators and the presence of *A.terrestris* in this study though.

Inhabitants often report *A.terrestris*' extinction on an island and later its recolonisation (Ursin, 1948b). Ursin (1948b) does however not believe that it is actually going extinct, but rather that *A.terrestris* fluctuates so intensely in population density from year to year that it is not observed by humans in its low years. The results obtained here do however indicate that there is some truth in the extinction-recolonisation theory, since the only variable significant to the presence of *A.terrestris* is the distance to nearest mainland. As with the other species affected mostly by distance this relationship cannot be explained by the smallness of the isolated islands, since there is a positive correlation between isolation and island size. The idea that *A.terrestris* is able to recolonise islands, even those situated at some distance from the mainland is supported by its very good swimming abilities (Ursin, 1952b) and its proposed ability to be transported between islands with floes of withered *Zostera marina* (common eelgrass) that is detached from the shore at unusual high tides (Ursin, 1950). The very dense populations on some islands have the effect that *A.terrestris* is dispersed much easier by stepping stone dispersal than direct from the mainland because there is a much higher probability of dispersal from an overpopulated island than from the much less densely populated mainland. As mentioned in the discussion of isolation effects, that is

probably why an isolated island like Ærø with many stepping stone islands in the South Funen archipelago houses *A.terrestris* when islands like Endelave and Samsø do not.

Common Shrew (*Sorex araneus*)

Sorex araneus was one of the first small mammals to immigrate to Denmark after the ice retreated. Bone findings have been dated to more than 13.000 years ago (Aaris-Sørensen, 1998). Thus it was present when the islands were isolated by the sea but still it is now only present on 11 of the 31 islands studied here. Traditionally shrews have been considered poor colonisers because of their high metabolic rates and small energy reserves, but according to Hanski (1986) this is a misconception. He finds that they actually are good swimmers and that they regularly immigrate to islands up to 1000 meters from the mainland. This is consistent with the fact that the distance to the nearest mainland is the only variable included in this study with significant explaining power for the presence of *S.araneus*. Apart from Bornholm, which is very likely large enough to have had a continuous population since its immigration to Denmark, the only islands where *S.araneus* is present are situated within 3300 m from the mainland. Thus a scenario of extinctions and recolonisations of *S.araneus* since the cease of the ice age seems very probable. To strengthen this *S.araneus* apparently is also capable of running several km over the ice in winter. Jensen (1993) cites an example from Sweden where a track from *S.araneus* had been followed for 4½ km over an ice and snow covered lake.

The number of catches per trap night for *S.araneus* is fairly small (0.072) and points towards a low population density of this species on the islands, with a resulting higher risk of extinction. All in all the evidence points towards a dynamic equilibrium of immigrations and extinctions for *S.araneus*, at least for the islands relatively close to the mainland. The low number of catches per trap night could however also be interpreted as a result of the behaviour of *S.araneus*. Being an insectivore it is not interested in the bait used here and would not enter a trap in search of food, but being at the same time very territorial (Jensen, 1993) it might enter traps out of inquisitiveness for new objects in its territory.

Sorex araneus is known to occur in many habitat types, but especially on meadows and tree-covered small biotopes (Jensen & Hansen, 2003). The catches made in this study confirm

that the distribution of *S.araneus* on the islands is about the same with 56% caught on permanent grassland and 22% in forest or hedgerows.

Pygmy Shrew (*Sorex minutus*)

Sorex minutus occurs only on three islands in this study and the logistic regression yielded no significant variables. The number of catches per trap night was very low (0.035). According to Muus (1993) it occurs in most parts of Denmark but in much lower densities than *S.araneus*. This and the fact that it has territories twice the size of *S.araneus* (Jensen, 1993) corroborates with the results obtained here and indicate a larger risk of extinction for *S.minutus* than for *S.araneus*. So although it was present in Denmark long before the isolation of the islands (Aaris-Sørensen, 1998) it is likely that it might go extinct on most islands but the largest ones. Two of the three islands where it is present are the two largest included here, Bornholm and Samsø. Hanski (1986) also found that *S.minutus* was less common on islands than *S.araneus* and attributed this to its poorer dispersal abilities than *S.araneus*.

Water shrew (*Neomys fodiens*)

Bone findings of *N.fodiens* in Denmark have been dated to around 7000 years old (Carlsen, 1995), but it is presumed to have immigrated much earlier around the same time as the other shrews *S.araneus* and *S.minutus* (Carlsen, 1995), (Aaris-Sørensen, 1998). Thus it was most likely present here when the islands were isolated. Still it is only present today on four of the 31 islands investigated in this study. This very limited distribution is probably the cause of the results in the logistic regression test, where no variables were significant in explaining the presence of *N.fodiens*.

Neomys fodiens is known for its close association with water, in which it hunts much of its prey (Jensen, 1993). Ponds and streams do however not have to be present in great quantities to facilitate the presence of *N.fodiens*. Three of the four islands where it is present do have a larger quantity of water biotopes than the mean of the islands included here, but it still covers only two to four percent of the land area and Bjørnø, which is a small island, has less than one percent water cover. Thus *N.fodiens* together with *C.glareolus* is a good example that a species can be present even where its favourite habitat is not present in large quantities.

Harvest mouse (*Micromys minutus*)

Micromys minutus is known for its ability to locally attain quite high densities (Jensen, 1993). It was found here on 11 of 31 islands with the relatively high density of 0.19 per trap night.

Micromys minutus is the latest known arrival of the small mammals included here. It was first recorded in southern Jutland less than 200 years ago and has since spread quite fast to the whole country. This fast dispersal has in the literature been ascribed more or less solely to *M.minutus*' ability to connect with humans and their transports of wood and animal food stuffs (Jensen, 1987). The results in this study do not corroborate with this. The only variable that comes out as significant in the logistic regression is the distance to the nearest mainland, so that the chance of encountering *M.musculus* is decreasing with isolation. Many of the islands where *M.minutus* is not found have the same or even more trafficking of humans and goods back and forth from the mainland and thus the presence-absence of *M.minutus* may not be ascribed only to human intervention but also to its own dispersal abilities or lack of same.

One thing that has to be taken into consideration when interpreting the results concerning *M.minutus* is the special behaviour of this species. In the summer months it lives mostly up in the vegetation and it rarely descends to the ground (Jensen, 1993). The trappability of *M.minutus* is thus very low in summer compared to the fall and winter months and the islands visited during summer or early fall could mistakenly be taken for void of *M.minutus*.

House mouse (*Mus musculus*)

Mus musculus is the most widespread of the species present on 26 islands. *Mus musculus* was first reported in Denmark around 2000-2500 years ago (Aaris-Sørensen, 1998) and thus it must have immigrated to all the islands where it is present today by its own accord or by human intervention.

The five islands where it is absent are all without permanent human residents, but not without other small mammal species, with Hjelm as the exception. This is consistent with results from Scotland where they found that *M.musculus* can only survive outside on islands with no human residents, when there are also no other small mammals (Berry & Tricker, 1969). It is also in accordance with the results of Hansen et al. (2003) where they found that *M.musculus* maintained a free living population in the wild on Anholt, where it is the only small mammal.

There are none of the inhabited islands where it is definitely absent, but there are a few where it is not very abundant. This is most likely as indicated by the studies of Berry and Tricker (1969) because of interspecific competition with other small mammal species present. *Mus musculus* is very sensitive to interspecific competition especially from *A.sylvaticus* where it is most often the weaker part (Hansen et al., 2003) and *A.sylvaticus* does also venture indoor in winter on some islands (*pers. obs*). In spite of *M.musculus*' close connection with humans (Hansen et al., 2003) the variable number of inhabitants does not have significant explaining power over the presence of *M.musculus*. The only variable that is significant is the Shannon index, which has a positive effect on the presence of *M.musculus*. A possible reason for this is that the Shannon index is positively correlated with the number of inhabitants but has less variation and thus will appear as the significant variable in a multiple regression test.

Yellow necked mouse (*Apodemus flavicollis*)

The first bone findings of *A.flavicollis* is dated to the boreal period more than 9000 years ago but it is presumed immigrated already in the pre boreal period (10250+ years ago) (Aaris-Sørensen, 1998). Thus it was present in Denmark long before most of the islands was isolated and probably also before the isolation of Bornholm where it is present today as one of only 5 islands in this study.

A part of the reason why this early immigrant is only present on 5 islands might be the size of its homerange. It ranges from a few hundred square meters to one ha and is generally considerably larger than those of the other small mammals (Jensen, 1993), (Hansen, 1997). Accordingly its population density will be lower than those of other species. This is consistent with the low catches of *A.flavicollis* in this study and also with the findings of (Hoffmeyer & Hansson, 1974) who finds that *A.flavicollis* has normally considerably lower population densities in southern Sweden than *A.sylvaticus*, its closest relative. A low population density on a small island will all else equal result in a larger risk of extinction by chance and if the species is then unable to recolonise the result will be as seen here. Why *A.flavicollis* should be a poor coloniser is unclear. It is a very mobile species that swims voluntarily (Jensen & Hansen, 2003), (Ursin, 1950) and though it is noted for its preference for forests and tree covered habitats, this habitat type does not seem to have to be present in large quantities to satisfy the needs of *A.flavicollis*. Three of the five islands where it is present are on the contrary quite poor on trees, with percentages much below the mean for all

islands. Many of the other islands which might seem very suitable for *A.flavicollis* because of their larger percentage of forests have however only been planted with these in the later years. They were formerly as tree less as most of the smaller Danish islands have been for the last couple of hundred years.

Two variables comes out as significant for the presence of *A.flavicollis* when a multiple regression test is carried out, but these are very much significantly correlated ($P < 0.004$) and when each is fitted Y by X separately with *A.flavicollis* none of them have significant explaining power. Number of inhabitants are very close to significant though ($P = 0.054$) and has a positive effect on the chance of meeting *A.flavicollis* on an island. This is most likely an indirect effect of the fact that number of inhabitants is highly positively correlated with island size and diversity (as measured by the Shannon index).

Wood mouse (*Apodemus sylvaticus*)

Apodemus sylvaticus is one of the most widespread mammals in Denmark both on the islands included in this study and in the rest of the country (Ursin, 1952a). It is also quite abundant where it occurs if the catches made here are taken as a measure of population density. In other words it is a species that is doing very well on the small islands. Grant (1970) claims that this success is a result of the generalist tendencies of the *Apodemus* genus. *Apodemus flavicollis* do however not confirm Grant's (1970) theory, since it is very restricted in its occurrence on the islands. There are several other reasons why *A.sylvaticus* should be so successful on the islands. The first is its ability to manage in the agricultural landscape. Hansen (1997) found that *A.sylvaticus* is an opportunist which is found in almost all nature types and that it was the species that were most often caught in cultivated fields. Like in the rest of the country cultivated land is the dominant nature type on most islands making for good opportunities for a species able to live there. The second reason is another aspect of *A.sylvaticus* habitat preferences. *Apodemus sylvaticus* is most frequently found on the forest edges (Telleria et al., 1991) and rarely in the heart of the forest. This is partly because it is ousted by *A.flavicollis* from this habitat when this species is present (Hansen, 1997). On the islands there are many hedgerows and other small tree covered habitats but rarely any forests of substantial size. Thus the distribution of threes and bushes on the islands makes them very suitable habitats for *A.sylvaticus*. The theory of competition between *A.flavicollis* and *A.sylvaticus* is justified here by the fact that the only island where they occur together is

Bornholm, by far the largest island included. The third reason for *A.sylvaticus*' success on islands is the fact that it does not fluctuate so violently in population sizes as for example *M.agrestis* (Ursin, 1952b). Thus the chances of *A.sylvaticus* going extinct by chance on a small island are not as great as it is for many other species of small mammals. The fourth reason has to do with *A.sylvaticus*' ability to disperse to islands. Both on the mainland and the islands *A.sylvaticus* is commonly found in coastal areas and it apparently has a preference for the thick shrubs of *Rosa rugosa* (rugosa rose), which is so common along the Danish coast (*pers.obs*). Thus it should (like *A.terrestris*) be able to be transported between islands with floes of withered *Zostera marina* (common eelgrass) that is detached from the shore at unusual high tides (Ursin, 1950).

Apodemus sylvaticus has two significant variables when a logistic regression test is carried out. These two variables the Shannon and the Simpson diversity indices are however highly positively correlated ($r=0.91$, $P<0.0001$) especially in the lower end of their range and this has the effect that when fitted Y by X alone; the Simpson index has no significant explaining power over the presence of *A.sylvaticus*. The reason for this is that there is a greater variation in the Simpson index values than in the Shannon index values and thus the Shannon index comes out as the significant variable. The Shannon index has a positive effect on the probability to encounter *A.sylvaticus*, i.e. the more diverse and island the better for *A.sylvaticus*. Adler and Wilson (1985) also found that an increase in habitat complexity had a positive effect on the probability of occurrence of *Peromyscus leucopus*, a close relative of *A.sylvaticus*.

Brown rat (*Rattus norvegicus*)

Rattus norvegicus is a late addition to the Danish fauna. It was first registered here in the early 18th century brought here with ships, possibly from Russia (Winge, 1908). The further dispersal of *R.norvegicus* throughout the Danish archipelago has very likely also taken place at least in part by human intervention, though it is a very able swimmer and is presumed to have its original habitat near the great rivers of Asia (Winge, 1908). There is also evidence to the fact that *R.norvegicus* is able to run substantial distances over the ice in winter. Ursin (1950) relates a story that one ran over to Bjørnø in the winter of 1946-7, a distance of 700 m.

The only significant variable in the logistic regression test is island size, which has a positive effect on the presence of *R.norvegicus*. The reason for this is most likely that island size is highly correlated with the number of inhabitants ($r=0.92$, $P<0.0001$). The more human inhabitants the more possibilities for this species which is closely associated with humans though it does not normally live in our houses like *M.musculus*. In a few cases *R.norvegicus* has been known to live independently of humans but it cannot withstand harsh winters (Jensen, 1982).

Conclusion

In this study I have shown that isolation is the most important variable in explaining the diversity of small mammals on the Danish islands, especially when the two species most dependent on humans are not included. Island size has no direct effect on the species diversity but is positively correlated with two of the three diversity measures applied (the Shannon index and total number of habitats) and thus exerts an indirect effect, since these two measures both have a positive effect on species diversity. The last diversity index, the Simpson is not correlated with islands size and is not well suited as a measure of an island's suitability for small mammals. This is because of its function as a dominance measure, where it has been shown here that a habitat type does not have to be present in large quantities to support a population of a species dependent on it. Isolation and habitat diversity are also the two variables that most often have a significant effect on the presence-absence of the 12 species, and to the same effect, with isolation as a negative influence and diversity (as measured by the Shannon index) as a positive.

The Danish archipelago as a whole does not seem to be a system in equilibrium. The "oceanic" islands are still poor on species and others like Bornholm are still oversaturated with species because the time elapsed since the last ice age are too short for the extinction rate to have had the time to create equilibrium.

The species of small mammals present in Denmark show a significantly nested distribution pattern and since ca. half of the species are significantly affected by island isolation the conclusion is that both differentiated dispersal abilities and differentiated extinction risks contribute to the creation of this distribution pattern.

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Appendices

Appendix 1 - Nature type distributions

Appendix 1. Proportions of naturetypes on the islands. The numbers does not in all cases add up to 100% since the method by which they are obtained is subject to some uncertainty. When used in tests numbers have been regulated to add up to 100%.

	Tree cover	Grass cover	Buildings	Agriculture	Moor	Water	Tidal meadow	Meadow	Common	Bog	Total
Agersø	4,68	6,19	4,00	52,01	0,00	2,74	26,62	1,86	0,73	1,63	100,46
Anholt	13,06	4,05	1,37	0,00	74,55	0,72	0,00	1,49	1,40	2,61	99,25
Avernakø	6,94	6,81	5,58	54,02	0,00	4,18	16,45	1,18	4,56	0,30	100,02
Barsø	10,88	14,14	1,38	58,48	0,00	0,37	7,88	1,06	5,20	1,29	100,68
Bjørnø	4,77	29,94	4,08	46,73	0,00	0,52	9,12	0,35	1,45	2,13	99,09
Bornholm	23,00	4,87	5,62	61,52	1,59	0,53	0,07	1,94	1,94	0,15	101,23
Baagø	5,93	5,46	2,28	61,27	0,00	2,51	16,68	1,02	1,51	2,48	99,15
Drejø	8,67	13,46	3,63	47,49	0,00	1,84	21,43	1,06	0,90	0,63	99,12
Egholm	4,38	6,84	1,65	68,96	0,00	1,03	10,49	5,11	0,00	0,88	99,33
Endelave	12,87	8,44	2,45	45,32	3,08	1,08	22,35	1,28	0,00	3,30	100,16
Fanø	17,63	8,13	4,31	7,45	29,35	0,54	16,16	1,84	5,42	10,05	100,86
Fur	16,02	14,66	5,07	48,73	5,07	0,62	5,84	1,39	1,68	2,18	101,25
Hesselø	28,34	43,68	0,54	0,00	0,00	2,00	23,12	0,00	2,01	1,01	100,69
Hjarnø	4,25	6,67	3,57	70,33	0,00	0,44	13,40	0,85	0,00	0,00	99,52
Hjelm	26,62	18,03	0,46	0,00	0,00	0,00	0,00	0,00	54,42	0,00	99,53
Lille okseø	63,57	33,83	1,63	0,00	0,00	0,00	0,00	0,00	0,00	0,00	99,04
Livø	19,89	7,90	0,78	25,52	4,31	0,85	23,30	0,32	15,53	1,93	100,33
Lyø	6,92	6,52	3,74	59,89	0,00	4,28	13,48	0,61	3,16	0,52	99,13
Læsø	30,65	5,28	3,45	20,14	20,59	1,84	14,32	0,00	0,00	2,82	99,08
Nexelø	7,48	19,19	1,96	31,90	0,00	3,27	8,58	0,00	25,50	2,60	100,48
Omø	6,47	8,70	7,09	49,61	0,67	2,61	23,82	0,00	1,08	0,30	100,36
Samsø	14,36	7,25	6,44	61,09	1,67	1,00	1,30	0,77	6,42	0,85	101,14
Sejerø	8,92	11,45	9,46	62,53	0,00	0,43	3,94	0,26	2,91	0,43	100,33
Skarø	4,12	12,47	3,13	56,23	0,00	0,42	15,14	8,10	0,00	0,00	99,61
St. Okseø	37,85	44,99	2,30	0,00	0,00	0,05	15,19	0,00	0,00	0,00	100,38
Vigelsø	20,32	27,01	0,29	0,00	0,00	0,48	50,95	0,00	0,25	0,00	99,30
Vorsø	54,28	24,89	0,18	0,00	0,00	1,12	15,28	0,00	0,00	4,31	100,06
Vorsø kalv	8,94	0,00	0,00	0,00	0,00	0,00	37,51	0,00	53,35	0,00	99,80
Æbelø	52,61	14,47	0,57	0,00	0,00	3,54	22,25	0,15	5,68	0,31	99,58
Ærø	8,45	4,05	8,73	69,10	0,00	0,38	3,47	5,18	1,13	0,54	101,03
Årø	8,48	19,42	3,14	43,84	0,00	2,34	16,55	1,84	0,14	4,49	100,23

Appendix 2 - Predator distribution

Appendix 2. Predators on the included islands. On all islands birds of prey have been observed.

Island	<i>Vulpes vulpes</i>	<i>Martes foina</i>	<i>Mustela erminea</i> / <i>nivalis</i>	Domestic cat
Agersø				x
Anholt				x
Avernakø	x	x	x	x
Barsø	x			x
Bjørnø	x	x	x	x
Bornholm	x			x
Baagø		x	x	x
Drejø		x		x
Egholm	x	x	x	x
Endelave	x			x
Fanø	x		x	x
Fur	x	x	x	x
Hesselø				
Hjarnø		x		x
Hjelm				
Ll. Okseø				
Livø	x	x	x	x
Lyø		x		x
Læsø	x			x
Nixelø				x
Omø				x
Samsø	x	x		x
Sejersø	x			x
Skarø		x	x	x
St. Okseø				
Vigelso			x	
Vorsø	x	x	x	
Vorsø Kalv	x	x		
Æbelø	x	x	x	
Ærø	x	x	x	x
Årø	x		x	x

Appendix 3 - Short descriptions of all islands

Agersø

Agersø was isolated from Zealand by the Littorina Sea about 8000 years ago (Pedersen et al., 1997). Like most of the Danish isles it was formerly abundant with forest, but now only a few small fragments of deciduous forest remain. The island is dominated by farmland (about 50% of the area) and tidal meadows (around 25%). Agersø has 255 permanent residents and some summer cottages. The island has no mammal predators but owls breed on the island.

Anholt

Anholt is one of the most isolated islands in the Danish archipelago. It is situated in the middle of Kattegat 45 km from the nearest mainland and was isolated by the coming of the Littorina Sea 8000 years ago. The island completely dominated by a large moor, that covers and 75% of the area. In subboreal times (3800-600 BC) most of this moor was covered by the sea and the island much smaller than now (Aaris-Sørensen, 1998). Of the remaining land 13% is covered by threes, mostly pine wood. Agriculture was given up on the island, by the 157 inhabitants, around 1960. Anholt has no mammal predators but owls are breeding on the island.

Avernakø

Avernakø was earlier two islands. They are now one, connected by an isthmus. Like the rest of the islands south of Funen it was isolated late around 4000 years ago (Hvidtfeldt, 1970), (Hansen, 1994). That is because it is situated south of the line that divides Denmark into a northern rising part and a southern sinking slowly into the underground since the termination of the last ice age. On top of that there are very low waters between the islands in the South Funen archipelago. Avernakø is one of the few small islands in Denmark that has remnants of the original forest. Otherwise it is dominated by farmland that covers around half the area, and tidal meadows. Avernakø is habited

Barsø

Barsø is a very hilly island situated off the east coast of southern Jutland, from which it was isolated by the coming of the Littorina Sea around 8000 years ago. The island has only a few fragments of forest, but many wide hedgerows all over the island. More than half of the area is farmland and the rest is mostly covered by permanent pastures and tidal meadows.

Bjørnø

Bjørnø is a small hilly island that is situated south of Funen. Like the rest of the South Funen archipelago it was isolated around 4000 years ago (Hvidtfeldt, 1970), (Hansen, 1994). Around half of the islands area is covered by farmland and a third by permanent pastures/grassland. There are only trees around the houses, in which the 33 inhabitants live in, and around the small bog in the middle of the island.

Bornholm

Bornholm is the largest island included in this study and the next most densely populated. It is also the first island in Denmark to be separated from the mainland, more than 10250 years old (Aaris-Sørensen, 1998). Bornholm is an agricultural island, with around 60% of the area

cultivated. Apart from that the landscape is dominated by several large forests, comprising almost 25% of the area.

Baagø

Baagø is quite flat and almost $\frac{3}{4}$ of the island was flooded in a large storm flood in 1872. Around 60 percent of the island is farmland and only small parts are tree covered, the main one being the large bog in the middle of the island. Baagø was isolated from Funen with the coming of the Littorina Sea around 8000 years ago.

Drejø

Drejø was formerly two islands, now connected by an isthmus. The western part is hilly, the eastern more flat. More than half of it was flooded in an 1872 storm flood. It is dominated by fertile farmland that covers just under half the area. The rest of the island is mostly tidal meadows and other permanent grassland. A few small forests are scattered over the island.

Egholm

Egholm is a very flat island that is situated near Aalborg. The flatness of the island means that, in spite of dikes, the island is a frequent victim of floods. It is formerly a part of the seabed and has only come into existence around 5000 years ago, because of the continuing isostatic rising of the land in the northern part of Denmark. It has therefore never been connected to the mainland in its present form, but the waters north of the island are very shallow, and when there are continuing easterly winds for a week or more the seabed is drained and the island almost connected with the mainland (*pers comm.* Holger Thomsen, farmer on Egholm). Egholm is dominated by agriculture, and almost 70% of the island is laid out to farming. The rest of the island is dominated by tidal meadows and permanent pastures, with only a few small scattered clumps of forest.

Endelave

Endelave is a varied island with less than half of the land occupied by agriculture and with two forests of some size and many hedgerows. More than $\frac{1}{5}$ of the area is tidal meadows. Endelave was isolated from Jutland around 7500 years ago by the Littorina Sea (Pedersen et al., 1997), but a bit later than many other islands because of the relative shallow waters between the island and the mainland. Shrews have been heard several times around the island (Laursen & Højager, 1989), but have not been caught by me.

Fanø

Fanø is one of the few Danish islands that have never been connected with the mainland. Around 5000 years ago the sea level rose to flood the land area now called the Wadden Sea. At the same time, along the old coastline, new small islands arose by deposition of the washed away materials. Those islands eventually grew together to form what is now known as Fanø (www.mitfanoe.dk). Only a minor part of Fanø is cultivated. More than half of the island is covered by moors and plantations, and the rest is dominated by tidal meadows and bogs.

Fur

Fur is a hilly and diverse island that contains all of the nature types included in this study. Around half the land is farmland, and wood cover and permanent pastures comprises

another 15% each. With the coming of the littorina sea Fur was isolated from mainland Jutland into 3 or 4 islands (Andersen & Sjørring, 1997) until the continuing isostatic rising of the Limfjord area reunited these into one.

Hesselø

Hesselø is a very isolated island situated in the middle of Kattegat. In 1983 it became the centre of a border dispute between Denmark and Sweden. It is privately owned, but is protected by EU. It was isolated early by the littorina sea, at least 8000 years ago (Nørrevang, 1969). The island has many hedgerows and small tree biotopes. There is no agriculture on the island.

Hjarnø

Hjarnø is a flat island situated at the mouth of the Horsens inlet. It is dominated by agriculture and more than 2/3 of the island is cultivated. The rest is mostly tidal meadows and other permanent grassland. There is one small forest on the island, but almost no hedgerows or other small wood covered habitats. Hjarnø is isolated a little later than the other islands in east Jutland, around 7000 years ago (Larsen & Kronborg, 1994), because of the shallow waters north of the island.

Hjelm

Hjelm is a small island situated south of Grenå. More than half of the island's area is protected common and the rest is divided between grass- and tree cover. Agriculture was abandoned on the island in the 1960's and the island is now left to natural succession. There are no permanent residents on Hjelm, but the owner lives there part of the year. There are no regular boats to the island and because of large boulders and tricky currents a change to a dinghy is required to enter the island. Hjelm houses a large colony of seagulls.

Lille Okseø

The next smallest island included in this study situated in the Flensburg inlet in southern Jutland; close to its sister island Store Okseø. Almost 2/3 of the island is covered in old forest and bushes and the rest is lawns around the buildings. There are no permanent human residents but it is used for camp schools. Lille Okseø is isolated as an island around 7500 years ago, a little later than the other south Jutland islands, because of shallow waters between the two Okseøerne and the mainland.

Livø

Livø is owned by the Danish state and the 25% of it that is cultivated is ecological. The rest of the island is very diverse with substantial amounts of forest, tidal meadows, heath and commons. Like the other Limfjord island Fur it was isolated around 8000 years ago (Andersen & Sjørring, 1997).

Lyø

Lyø is about 6000 years old as an island (Larsen, 2001). It was the first of the South Funen islands to be isolated because of the deep waters between Lyø and the mainland. Around 60% of the island is cultivated and the rest is mostly divided between tidal meadows and other permanent grassland. There are many trees around the houses and a couple of small forests, one of them planted within the last 15 years.

Læsø

Læsø is the youngest of the islands in this study. The Littorina Sea flooded the area where Læsø is now, and it was not until around 2700 years ago that sand depositions made Læsø rise above the sea (Hansen, 1994). Two hundred years ago Læsø was almost completely tree less, but in 1930 the Danish state started to replant and now 30% of the island is tree covered, mostly with Scots pine. Only 1/5 of the island is cultivated and much of the rest is protected moors and tidal meadows.

Nexelø

This hilly island has a very varied nature. About 1/3 of the island is cultivated, a good part of that ecologically. The rest of the island is dominated by §3 protected commons and other grassland, but there is a small regular forest and several lakes. Nexelø was isolated from Zealand 8000 years ago.

Omø

This island has two parts, one hilly cultivated northern part and a flat southern part with large tidal meadow areas and a large lake in the middle. Half the land is cultivated. Omø was isolated 8000 years ago by the Littorina Sea (Pedersen et al., 1997).

Samsø

Samsø is the second largest island included in this study. It is comprised by a northern part, of which large parts are protected common, and a southern part which is mostly farmland. 60% of the area is cultivated and there are two large forests on the island. It was isolated from Jutland around 7500 years ago by the Littorina Sea, a little later than some of the Danish islands because of shallow waters between the island and the mainland coast.

Sejerø

Sejerø was isolated by the coming of the Littorina Sea 8000 years ago. It is an agricultural island with more than 60% of the land cultivated. There are a few small forests. There is some disagreement between the inhabitants as to whether there are foxes on the island or not.

Skarø

Skarø is quite flat and a large storm flood in 1872 flooded the island almost completely for a short time. It is an agricultural island with more than half the area cultivated. A large part of it is ecological. There are very few trees on the island and the non cultivated parts are mostly tidal meadows and other forms of permanent grassland. Skarø is isolated around 4000 years ago together with the other south Funen islands (Ursin, 1949).

Store Okseø

Store Okseø is a small island situate in the Flensburg inlet in southern Jutland. The island has no permanent human residents or mammal predators, but there is a summer restaurant on the island, and the tenants of this have dogs and cats. Store Okseø is quite hilly and dominated by a large, formerly cattle grazed, meadow. The rest of the island is tree covered and the northern part a large tidal meadow. Store Okseø is, like Lille Okseø, isolated from the mainland around 7500 years ago.

Vigelsø

Vigelsø is a flat state owned island situated in the Odense inlet. It was isolated around 7500 years ago. Most of the island is a protected bird sanctuary. The protected part of the island is tidal meadows and permanent pastures. On the rest of the island, 25 ha have been planted with deciduous trees within the last 15 years. There is no agriculture on the island. It was given up in 1990, when the state bought the island. Stoats have been put out to keep the rat population down.

Vorsø

Vorsø is a small island situated in the Horsens inlet in eastern Jutland. It was bought by the zoologist Herluf Winge in 1928. Most of the agriculture was given up and it was laid out as a refuge for the wildlife. In 1979 the Danish state took over the island, the remaining agriculture was given up and since then the island has been left to natural succession. More than half of the island is tree covered and most of the rest is permanent grassland and tidal meadows. Vorsø together with Vorsø Kalv is isolated as an island around 7000 years ago, a little later than other islands because of the shallow waters between the islands and the mainland.

Vorsø Kalv

Vorsø Kalv is the smallest island included in this study. It is situated close to Vorsø, till which it is possible to wade through the water. Most of the island is protected common and tidal meadows.

Æbelø

Æbelø was bought by a foundation in 1996 and protected by law. About half of the island is old forest in which there are several small lakes and bogs. The other half is all grass covered in one form or another, and there is no agriculture on the island. Æbelø is connected to Funen when the tide is very low. It was isolated with the coming of the Littorina Sea 8000 years ago (Larsen, 2001).

Ærø

Ærø is a large agricultural dominated island. More than 2/3 of the island is cultivated and the island is the most densely populated island in this study. The very hilly island is quite isolated with more 11 km to the South Funen coast.

Årø

Årø is a flat 566 ha large island, that is situated around 500 m off the mainland in southern Lillebælt. It was isolated by the coming of the Littorina Sea around 8000 years ago. Because of the flatness Årø was almost completely flooded by the large storm flood in 1872. It is a diverse island, with less than 45% of the area cultivated and with several bogs, tidal meadows and permanent grassland. 25 years ago there was only very little tree cover on the island, but since then two forests have been planted.

Appendix 4 - Correlation values for all variables

