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# **Estimating and analysing the occupancy of the introduced shrew *Crocidura russula* in Norway.**

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## Abstract

*The Greater white-toothed shrew (Crocidura russula)* is a shrew that was discovered in Norway in 2017. The species is of concern because it is invasive and has a history of environmental impact. It is native around the Mediterranean Sea and in Continental Western Europe. It was discovered in Ireland in 2008, with a subsequent decline in the only native shrew. To study the spatial distribution of the species in Norway, fieldwork was conducted in the Stavanger region in 2019. The field survey consisted of camera trapping, pitfall traps, and confirmed reports from local citizens. *Crocidura russula* was discovered in 19 of 83 camera trapping stations, with an occupancy probability of 0.248 (CI = 0.248 - 0.404). The occupancy probability was similar to the native species *Microtus agrestis*, *Sorex araneus*, and *Sorex minutus*. The detection probability estimate was the highest of all species observed. Several covariates were tested to explain variation in occupancy. In the best model detection probability significantly decreased with increasing solar altitude, and increased with increasing proportion of artificial, open, and forest habitat. In the top ranked occupancy model human population had a positive effect, while the amount of forest at the landscape level negatively affected occupancy. The results had a large degree of uncertainty, and no predictor significantly predicted occupancy probability for *Crocidura russula*. There was also no support for a suspected point source at Stavanger port. No negative impact of *Crocidura russula* was found in this study, but this may be due to the limited sample size. More research is needed to assess how and whether *Crocidura russula* is expanding, and increased sample area and multi-season sampling should be a priority.

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# 1. Introduction

In recent years invasive species have become a larger problem, and the annual rate of new introductions has continually increased during the last 200 years (Seebens et al., 2017), with 37% of first records occurring between 1970 and 2014. One of the main reasons for the increasing numbers of invasive species is global trade, as a country's number of invasive species is closely associated with the degree of international trade (Westphal et al., 2008). Invasive insects have been estimated to cost at least 76.9 billion USD annually by reducing ecosystem services, human health, goods and services and biodiversity (Bradshaw et al., 2016) and invasive agricultural pests are a major threat to global food security (Paini et al., 2016). Introduced species can also reduce biodiversity, and threaten native species through hybridization, competition, and parasitism (Hulme et al., 2009).

In 2012 a new invasive mammal was reported in Norway; the greater white-toothed shrew (*Crocidura russula*). In 2017, more individuals were discovered, and it was recognized as a new established species. The species is native to Western Europe and Northern Africa and has probably been introduced to Jæren in Norway by freight transport from Central Europe (Hansen & Bækkeliën, 2019). For now, *Crocidura russula* is not listed on the Norwegian Alien Species List (Artsdatabanken, 2018), and more knowledge about the species in Norway is vital. Understanding the spatial distribution of invasive species is crucial if we want to minimize their impact on native ecosystems, understand the dynamics that shape their spread, as well as to predict what their ecological impact will be.

Previous *Crocidura russula* invasions or range expansions have had dramatic impacts on other species. In Switzerland, *Crocidura russula* increased its range 25 kilometres northward between 1975 and 2000 (Vogel et al., 2002). This caused the local extinction of the closely related bicolored shrew (*Crocidura leucodon*), confirmed by trapping and owl pellet analysis. Similarly, the pygmy shrew (*Sorex minutus*) is almost completely absent from areas where *Crocidura russula* is established in Ireland (McDevitt et al., 2014). Assuming that *Sorex minutus* was present prior to the arrival of *Crocidura russula*, this suggests a highly negative impact. Both results show the destructive impact *Crocidura russula* can have on wildlife. However, the impact in Norway may be different, as the country has more diverse landscapes and more native shrew species than Ireland. Nevertheless, the results from Switzerland may suggest that *Crocidura russula* could outcompete similar species even in a country with heterogeneous landscape and a larger shrew diversity. Since *Crocidura russula* is highly

anthropophilic and temperature-limited, it is unlikely that it will spread to areas far from human infrastructure or to upland habitats.

In addition to potentially outcompeting native species, invasive species can also function as vectors for new, emergent diseases. In Ireland, *Crocidura russula* has been found to be a reservoir host for a novel serovar of the pathogenic bacteria *Leptospira* (Nally et al., 2016). *Leptospira spp.* causes the acute disease Leptospirosis, most often transmitted through contact with the urine from infected individuals (Mayer-Scholl et al., 2014). Some *Leptospira* serovars can be lethal in non-reservoir hosts (Nally et al., 2016), and such pathogens may be a serious problem in naïve populations, where the invasive species gains an advantage by being more resistant (Strauss et al., 2012). One example of such disease mediated invasions is the introduction of the grey squirrel (*Sciurus carolinensis*) to Europe. The grey squirrel acts as a carrier for the squirrel poxvirus (SQPV), which is non-lethal in grey squirrels but highly increases the mortality of native red squirrels (*Sciurus vulgaris*). Studies have estimated that the displacement of red squirrels by grey squirrels is 17 to 25 times faster in the presence of squirrel poxvirus (Sandro, 2008), thereby causing dramatic declines in red squirrel populations. In addition to its effects on wildlife, Leptospirosis is a major public health problem in many countries (Bharti et al., 2003), and novel serovars could potentially be an added risk to humans. This is especially relevant as *Crocidura russula* is highly associated with human settlements. Taken together, these studies highlight the disease risk of invasive species such as *Crocidura russula*, with potential consequences for both native wildlife and public health.

Results from Ireland show that *Crocidura russula* is spreading fast, giving native wildlife little time to adapt to its establishment (McDevitt et al., 2014). From 2008 to 2013 the species had a radial expansion of 5.5 km annually, and the main distribution range amounted to 7 600 km<sup>2</sup> in 2013. The speed of expansion limits the ability of native species to adapt to new habitats and niches, and probably increases the negative ecological impact.

There are several potential explanations for the quick spread and competitive dominance of *Crocidura russula*. Unlike most European shrews, *Crocidura russula* is heterothermic and able to enter torpor, a state where metabolism is extremely low, and this gives it an advantage in areas where it alone has this adaptation (Nagel, 1977). This allows the species to endure unfavourable climatic and dietary conditions with lessened energy losses. Nowack and Dausmann (2015) have proposed that heterothermy facilitates colonization of new habitats by

allowing individuals to arrive in new areas in relatively healthy condition. *Crocidura russula* is also more social than shrews native to Norway and can attain higher population densities, especially during the winter (Cantoni, 1993; Genoud, 1985). Their high densities help reduce energy expenditure substantially, through nest huddling. The higher densities may also overrun existing shrew species through competition for food, shelter, and suitable nests.

It is clear that the greater-white toothed shrew can have dramatic impacts on native wildlife, in addition to potentially being a public health risk. Assessing and quantifying its spatial distribution in Norway are important prerequisites for mitigating ecological impacts.

The present study aimed to understand what factors affect the occupancy and detection probability of *Crocidura russula* in Norway by using occupancy models accounting for imperfect detections to test the effect of different predictors, while also comparing with results for native species. Predictors consisted of habitat covariates at three different scales, human population density, in addition to distance to transport, built-up areas, and the suspected point-source location in Stavanger port.

## 2. Material and methods

### 2.1 Study area

The study area is the region around Stavanger and Jæren in Rogaland county, in the southwest of Norway (Fig. 1). This is where *Crocidura russula* was first detected in Norway. The area is about 619 km<sup>2</sup> (MCP, 95%). The camera traps took photos in 83 different locations, ranging from 64.9 to 65.5 degrees N and 29.9 to 31.9 degrees E, and from 2 to 200 meters above sea level. The confirmed observations originated from approximately the same area.

The area has an oceanic climate, with mild winters and temperate summers. The landscape is flat and dominated by farmland. The region is one of the most populous in the country, and Norway's third largest city Stavanger/Sandnes is in the northern part, with a population of 228 287 (Statistics Norway, [ssb.no](https://www.ssb.no)). Most of the area falls within the boreo-nemoral vegetation zone (Moen, 1998), which is characterized by the transition between temperate forests and conifer-dominated forests. Temperate deciduous species such as sessile oak (*Quercus petraea*), European oak (*Quercus robur*), small-leaved linden (*Tilia cordata*),

common hazel (*Corylus avellana*), and European ash (*Fraxinus excelsior*) dominate in sunny slopes with good soil, while the rest of the forest landscape mostly consists of birch (*Betula* spp.), grey alder (*Alnus incana*), and conifers. Due to the small size of the study area, there is little variation in climate. Stavanger in the north had a mean annual precipitation and mean annual temperature of 1 428 mm and 8.9 C in 2019, while Obrestad fyr further south had 1 302 mm and 8.1 C (<http://seklima.met.no>).

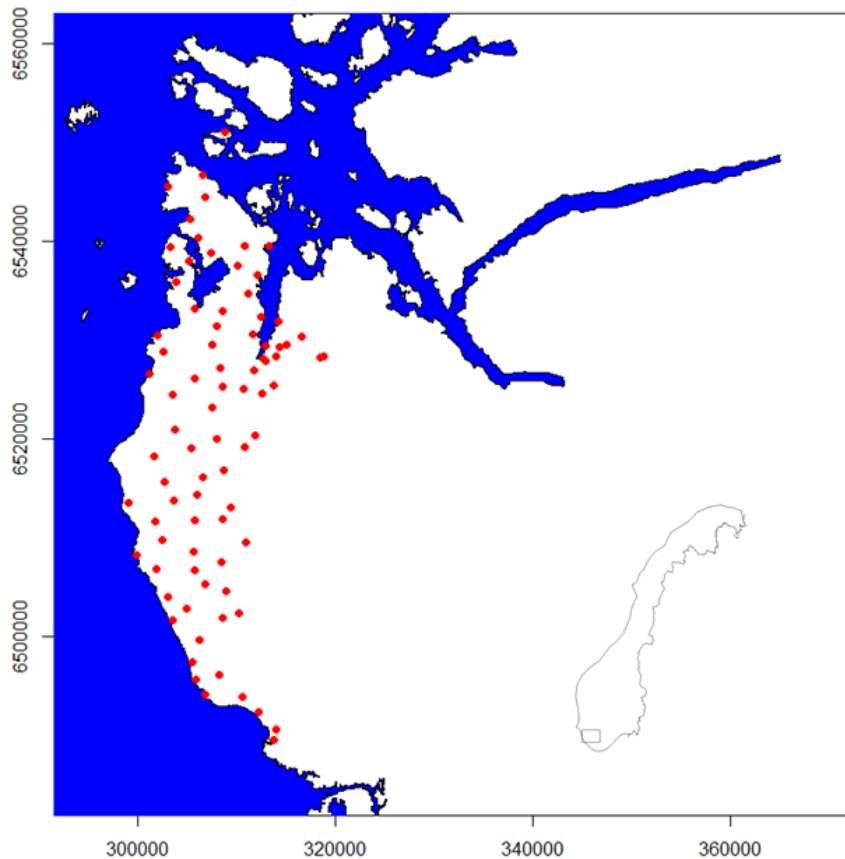


Figure 1. Map showing the study area, with camera traps shown in red. The study area's location in Norway is shown in the inset.

## 2. 2 Study species

The greater white-toothed shrew (*Crocidura russula*) (Fig. 2) is a shrew native to Northern Africa and Western Europe (SARÀ & VOGEL, 1996). Brändli et al. (2005) suggest that the species first arrived in Europe from Morocco approximately 38 000 years ago and arrived in the Canary Islands during the last 500 years (Molina et al., 2003). In addition, it has recently been introduced to Ireland (Tosh et al., 2008). The species is widespread within its native

range (Balloux et al., 1998) and is listed as *least concern* (LC) on the International Red List (Aulagnier et al., 2016).

*Crocidura russula* are medium-sized shrews, with a weight of between 11 and 14 g (Balloux et al., 1998). They are also monogamous (Cantoni & Vogel, 1989), with pairs defending territories of about 100 m<sup>2</sup>. Pairs typically produce between 3 and 4 litters consisting of between two and nine young. Unusually for mammals, natal dispersal is female-biased and limited to the first-litter juveniles (Favre et al., 1997).

The species probably evolved in Africa and moved northward as glaciers retreated (Brändli et al., 2005). As such, their distribution is probably limited by temperature (Torre et al., 2014). In the northernmost parts of its distribution, *Crocidura russula* is dependent on humans for winter survival, both for food and shelter from the cold (Balloux et al., 1998). For this reason, they often occur around human settlements and infrastructure.

As with other shrews, *Crocidura russula* has a high metabolism and suffers high mortality rates during winter. However, it has a better ability to downregulate metabolism during winter and could thus have an advantage over red toothed shrews (Nagel, 1977; Nowack & Dausmann, 2015). Since no other white-toothed shrew occurs in Norway, this gives them a unique advantage.

*Crocidura russula* is mainly an insectivore and is also a typical generalist and opportunist, with a diet strongly depending on available food sources (Brahmi et al., 2012). In Algeria their diet was found to consist mostly of insects (49% of biomass), centipedes (29.7%) and lizards (14.9%), with small inputs from plants, isopods, arachnids and snails (Brahmi et al., 2012). On the other hand, results from Europe show a much higher prevalence of plant material, probably representing a local adaptation to insufficient insect availability (Bever, 1983 in Brahmi et al., 2012).

*Crocidura russula* is preyed upon by other species, and has been documented in pellets from barn owls (*Tyto alba*) and common kestrels (*Falco tinnunculus*) (Tosh et al., 2008), and in guts and scats from the European polecat (*Mustela putorius*), stone marten (*Martes foina*) and pine marten (*M. martes*) (Baghli et al., 2002; McDevitt et al., 2014). The importance of *Crocidura russula* as food for other species is poorly understood.



Four other species were also studied (Fig. 3): wood mouse (*Apodemus sylvaticus*), field vole (*Microtus agrestis*), Eurasian shrew (*Sorex araneus*), and Eurasian pygmy shrew (*Sorex minutus*).



Figure 2. van der Kooij, J. (2019). Picture of a mature *Crocidura russula* individual.



Figure 3. van der Kooij, J. Pictures of a) *Apodemus sylvaticus* (2015), b) *Microtus agrestis* (2017), c) *Sorex araneus* (2011), and d) *Sorex minutus* (2015).

## 2.3 Data collection

The data were collected using three different methods: camera trapping, pitfall trapping and collecting observations from the public (citizen science). The methods used for camera and pitfall trapping follow the methodology described in van der Kooij and Møller (2018).

Camera trapping was performed between August 9th and October 7th 2019, and makes up the main part of the information used in this study. The camera traps were active for two days, with a few operating longer due to practicalities. 23 different cameras were used, in a total of 83 locations (Fig. 1). The cameras were mounted on a stand together with a feeding box containing moss and mealworms. The stand was then buried with the top of the feeding box just above ground level, the set-up is shown in Figure 3. This method assures both a fixed distance between the camera and feeding box and a constant angle between them. The cameras took five snapshots when motion sensors were activated, each with a one second interval. During night-time infrared flash was used. In addition, coordinates, elevation, habitat description, camera information and trapping date were recorded for each location.

Pitfall and Heslinga trap data contain information about 38 different trapping events. Pitfall traps were made up of two buckets, with the first bucket buried in the ground and the other inside the first. The purpose of the second bucket was to divert water from the first bucket. A plastic lid was placed approximately 12 centimetres above the buckets, using metal sticks to keep it up. This was to protect against rain and predators. The buckets were checked daily and the species of captured individuals determined. Heslinga traps were also used, these capture small rodents alive inside a small cage containing hay and mealworms. The traps were checked three times daily.

The public was informed about the study through both newspapers and television and asked to report observations of *Crocidura russula*. The reports consisted of photos, videos, and dead animals, which were then identified by Jeroen van der Kooij. The data includes geographical coordinates, sighting date, locality name, and the number of individuals reported.

## 2.4 Predictors of detection and occupancy

Information about habitat types was derived from AR5, a comprehensive map dataset published by the Norwegian Institute of Bioeconomy Research (NIBIO). AR5 separates between 11 habitat types: built-up areas, transport structures, tilled fields, untilled fields, pastures, forests, open solid ground, peatlands, glaciers, freshwater, and ocean (Ahlstrøm et al., 2019). The minimum mapping unit is 500 m<sup>2</sup> for agricultural areas and 2000 m<sup>2</sup> for the other habitat types. In addition, information about the location of Stavanger port and the ocean was derived from CORINE Land Cover Inventory for 2018, which has a minimum mapping unit of 250 000 m<sup>2</sup> for areal phenomena.

To calculate habitat measures I made circular buffers around each camera site at three scales, 1 m, 15 m, and 800 m radius. The 1 m radius represents the habitat directly around the camera site. The 15 m radius corresponds to *Crocidura russula*'s home range size, which Genoud (1988) reported as being between 102 and 182 m<sup>2</sup> (5.7 – 7.6 m radius), I set it to 15 m to ensure that the home range of the detected shrews fell within the area and to account for the large uncertainties in the home range estimates. The 800 m radius corresponds to *Crocidura russula*'s assumed mean dispersal distance (Jaquiéry et al., 2008). I then measured the proportion of different habitat types inside each of the polygons. For the detection models, built-up areas and transport structures were combined as artificial habitat, while tilled and untilled fields were combined as crops for the occupancy models.

Human population density was derived from Statistics Norway's 1 km<sup>2</sup> population grid for 2019. The number of people is derived from the National Population Register coupled with the cadastre, summarized for gridded squares of 1000 m x 1000 m. Three camera sites fell just outside of the grids, and for these the population density of the closest grid was used.

In addition to the habitat measures, I calculated distances to features. The distance-based predictors were calculated using two approaches. For the detection predictors, distance to port, and distance to ocean, I calculated the shortest Euclidean distance from the camera site to the habitat type in question. For the occupancy predictors, I measured the distance from the centre of 5 x 5 m grid cells within each 15 m polygon to the habitat type in question. An example of a grid is given in Figure 2. This allowed me to calculate the average distance from the home range, and not just from the camera site. Distance to Stavanger port was included as this is the suspected point source.

The camera trapping was conducted between August and October, and the dates differed between the sites. To account for differing day lengths, solar altitude was added to the detection models. Solar altitude is the angle of the sun in relation to the horizon, with 0 representing sunrise and sunset, negative values representing nighttime and positive values representing daytime. The solar altitude (in radians) was calculated for each camera site for each occasion.

An overview of the predictors used in the occupancy and detection models is given in Table 1.

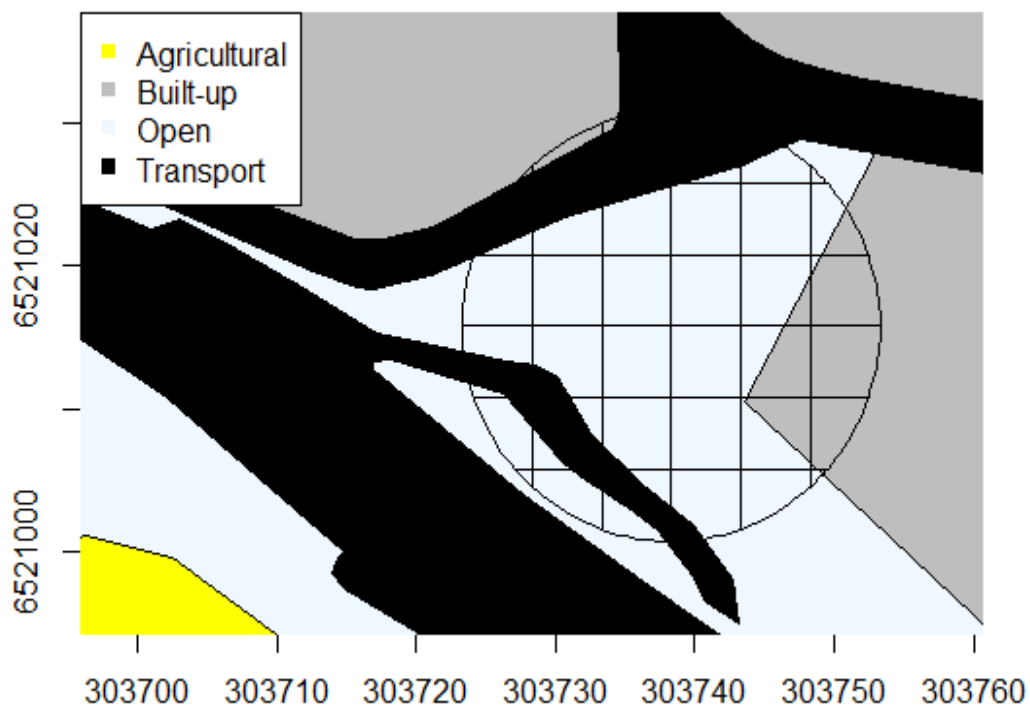


Figure 3. Figure showing an example of a grid created to measure the average distance to a habitat type. Each grid cell is 5 m x 5 m, except the cropped ones at the edge. The distance was calculated from the centre of each grid cell to the closest focal habitat, and then averaged across all cells. This gave an average distance for each site.



Figure 4. van der Kooij, Jeroen (2018). Photograph showing the camera trap set-up.

Table 1. Overview of the predictor variables used in the detection and occupancy models.

	Predictor	Note	Transformation
Detection	Habitat types	Proportion of habitat within 1 m polygons	
	Artificial		Natural logarithm
	Forest		Natural logarithm
	Open		Natural logarithm

Other		
Distance to transport	Euclidean distance in km	Natural logarithm
Distance to built-up	Euclidean distance in km	Natural logarithm
Solar altitude		None
Occupancy		
Habitat types	Percentage of habitat within 15 m and 800 m polygons	
Built-up		None
Crops		None
Forest		None
Pasture		None
Transport		None
Other		
Distance to transport	Average distance to transport in m	None
Population	Human population density within 1 km <sup>2</sup> grids	Natural logarithm
Distance to ocean	Euclidean distance in km	None

## 2.5 Statistical analysis

I used single season occupancy models to estimate what factors affect the occupancy of five different species of small mammals at camera trap sites, with a focus on *Crocidura russula*. Occupancy can be interpreted as the proportion of sites occupied by a species. This approach assumes that sites are occupied by the species of interest during the entire season, that no new sites become occupied, that there are no false positives and that detection at one site is independent of detection at others (MacKenzie et al., 2002). Occupancy models are hierarchical models that account for imperfect and potentially biased detections.

I used the camera trapping data to create detection histories for the five study species, with one hour serving as the occasion unit. Pitfall trap data was excluded due to low numbers of observations. For every species, the detection histories contain information on the detection and non-detection during every occasion unit, for all camera trapping sites. The “occu” function from “unmarked” (Fiske & Chandler, 2011) was then used to fit the single season occupancy model of MacKenzie et al. (2002) on the detection histories.

The occupancy model consists of two submodels, the first one models the observation process, while the second models the state process. For a given site  $z_i$ , occupancy can be modelled as:

$$z_i \sim \text{Bernoulli}(\psi_i)$$

where  $\psi_i$  is the probability of occurrence at the site, while the observation process can be modelled as:

$$y_{ij}|z_i \sim \text{Bernoulli}(z_i p_{ij})$$

where  $p_{ij}$  is the probability of detection at site  $i$  at occasion  $j$ . Covariates can be modelled as:

$$f = \log\left(\frac{\psi}{1 - \psi}\right) = x'\beta$$

Where  $f$  is the log odds of a species occupying the site,  $\beta$  is a vector of parameters, and  $x$  is a vector of the covariates. This allows us to account for temporal and spatial covariates which affect detection and occupancy.

The detection models were created by combining all combinations of the detection covariates with a maximum of three terms. The proportion of artificial habitat was removed from *Microtus agrestis*, *Sorex araneus*, and *Sorex minutus* models as these had identifiability issues. This resulted in 15 candidate models for these species, and 26 candidate models for *Crocidura russula* and *Apodemus sylvaticus*. The models were ranked according to the Akaike Information Criterion adjusted for small sample sizes,  $AIC_c$ , (Burnham & Anderson, 2004). The top ranked detection model for each species was then used in the occupancy models.

To determine the best ranked occupancy model, I used a multi-step process, with a forward stepwise selection. I first modelled the effect of all single variables on the occupancy and retained the variables that had a lower  $AIC_c$  than the null model. For *Sorex araneus*, the two top ranked predictors had a cumulative weight of 1, and in this case only these were retained. All combinations of these predictors were modelled, with a maximum number of three terms per model. This resulted in 26 candidate models for *Crocidura russula*, 16 for *Apodemus sylvaticus*, 35 for *Microtus agrestis*, 16 for *Sorex araneus* and 50 for *Sorex minutus*. These models were also ranked by the  $AIC_c$ . Models within  $2 \Delta AIC_c$  of the best model were averaged to account for uncertainty in the model selection.

To analyse the effect of *Crocidura russula* on native species, I fitted the co-occupancy model of Rota et al. (2016), using the significant predictors of occupancy and detection for each species as identified through model-averaging. In addition, I used simple linear regression to test the effect of *Crocidura russula* presence and activity on the activity of the four other study species. Activity was defined as the number of photos taken per event, with an event



being a separate visit to the camera trap. Two visits were defined as separate if more than 9 minutes passed between them.

### 3. Results

The camera trapping stations were active for a total of 179 trapping days at 83 sites (mean = 2.16, Fig. 1). In total, 20 different species were identified (Table A1), with a combined number of observations of 1259 (mean = 69.25). 48 animals were not identified to species level. *Apodemus sylvaticus* was the most frequently detected species (Table 2), accounting for 50.12 % of all confirmed observations. Models were only fitted for *Crocidura russula*, *Apodemus sylvaticus*, *Microtus agrestis*, *Sorex araneus*, and *Sorex minutus*, as the other species had very few observations (<10).

Table 2. Summary statistics for the camera trapping data.

	Number of observations	Number of occupied sites
<i>Crocidura russula</i>	229	19
<i>Apodemus sylvaticus</i>	631	54
<i>Microtus agrestis</i>	36	11
<i>Sorex araneus</i>	240	27
<i>Sorex minutus</i>	40	8

The pitfall and Heslinga trapping stations had a total of 125 trap days (mean = 3.38 active days per trap). Ten traps successfully detected animals (0.26), while 28 remained empty (Fig. 5). The pitfall traps accounted for nine of the detections, while the Heslinga traps caught nine animals. Four different species were captured: *Sorex araneus*, *Crocidura russula*, *Apodemus sylvaticus*, and *Sorex minutus*. The confirmed reports contained 60 certain observations of

*Crocidura russula*, 6 unsure, and one each of *Sorex araneus* and *Sorex minutus* (Fig. 5). The combined detections for each study species are shown in Figure 6.

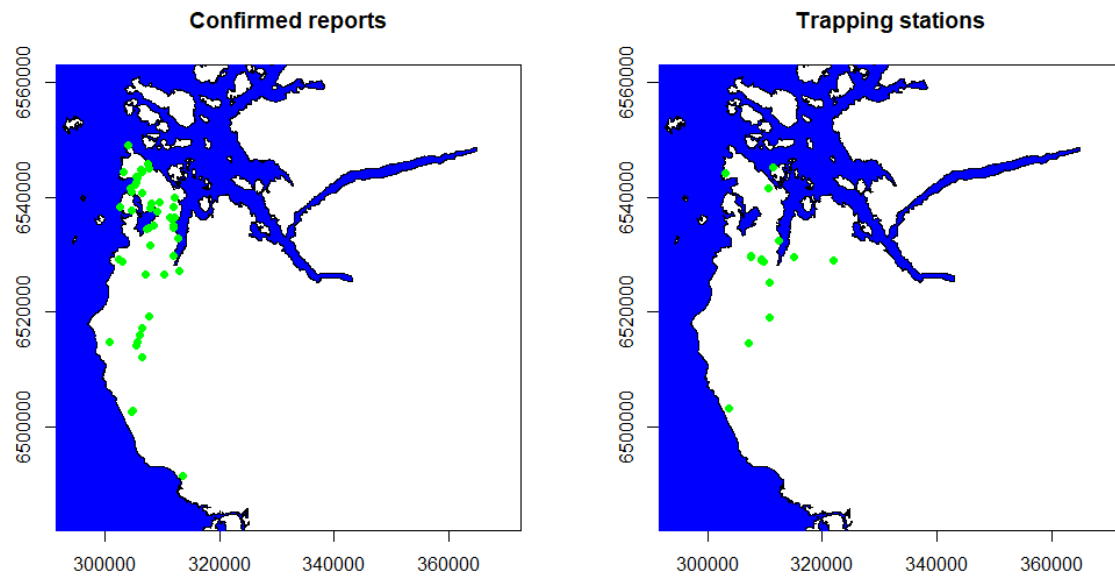


Figure 5. The locations of the confirmed reports and trapping stations.

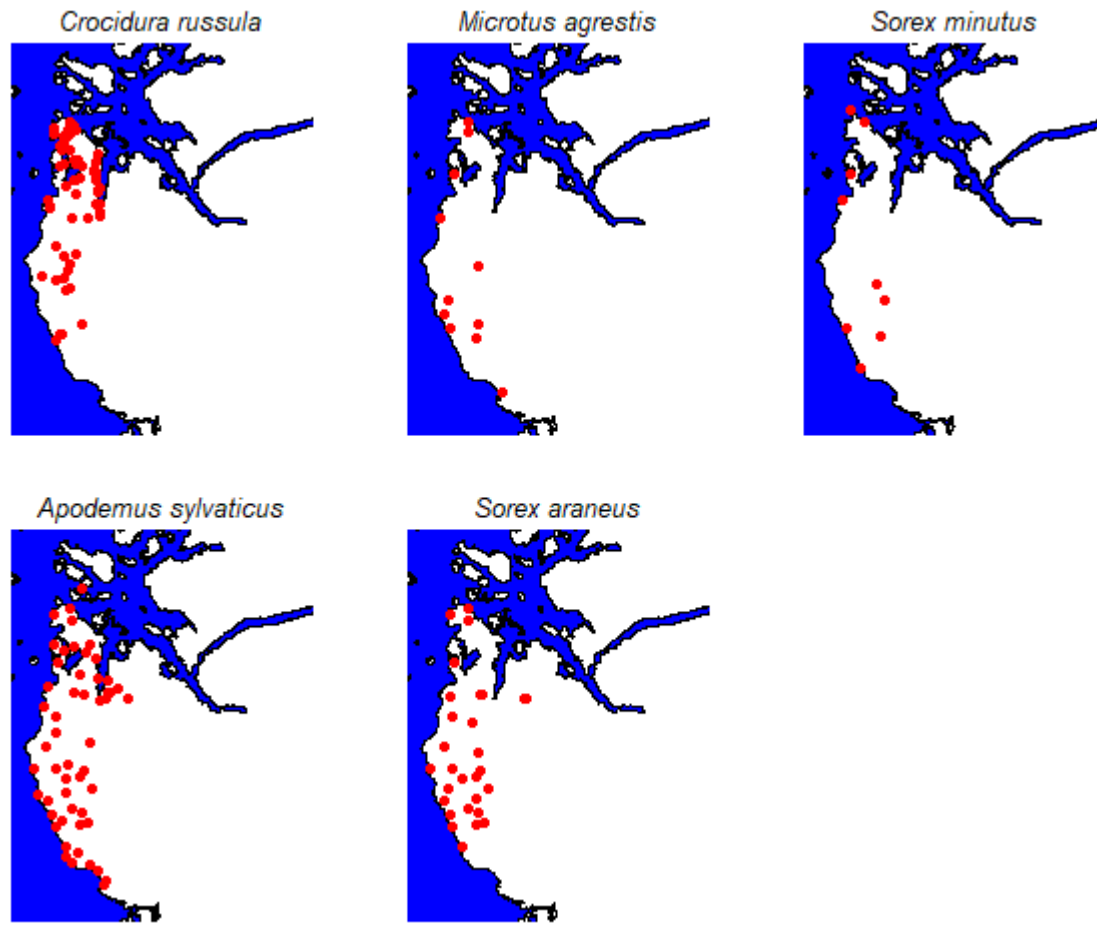


Figure 6. Location of detections for each study species, using data from camera trapping, confirmed reports, and trapping stations.

### 3. 1 Occupancy and detection estimates

*Crocidura russula* had a higher detection probability than the other species ( $p = 0.47$ , CI = 0.343 - 0.603; Table 3). The other species had similar detection probabilities, except *Microtus agrestis* which was smaller than *Apodemus sylvaticus* and *Sorex araneus*. *Crocidura russula* had the second highest occupancy rate after *Apodemus sylvaticus*, but the confidence intervals overlapped for all species except *Apodemus sylvaticus* (Table 3).

Table 3. Occupancy and detection estimates for the study species, with the 95 % confidence interval in parenthesis. Estimates are based on model-averaged predictions using mean values for all predictors.

	Occupancy	Detection
<i>Crocidura russula</i>	0.248 (0.136-0.404)	0.471 (0.343-0.603)
<i>Apodemus sylvaticus</i>	0.756 (0.630-0.849)	0.082 (0.052-0.127)
<i>Sorex araneus</i>	0.075 (0.025-0.212)	0.095 (0.067-0.131)
<i>Sorex minutus</i>	0.017 (0.002-0.160)	0.050 (0.022-0.107)
<i>Microtus agrestis</i>	0.042 (0.002-0.485)	0.014 (0.004-0.048)

### 3. 2 Model selection results

#### *Crocidura russula*

The top ranked model for predicting the occupancy of *Crocidura russula* contained population and forest (800 m) as predictors (Table 4). Nine other models had comparable support ( $\Delta AIC_c < 2$ ). Six of these models contained population as a covariate, six included the distance to ocean, four contained forest (800 m), and three contained distance to transport. The top ranked model for estimating *Crocidura russula* detection probabilities included solar altitude, proportion of artificial habitat, forest habitat, and open habitat as covariates (Table 5). No other model had support.

#### *Apodemus sylvaticus*

The top ranked model explaining *Apodemus sylvaticus* occupancy included distance to port and crops (15 m) as predictors (Table 4). One other model had  $\Delta AIC_c < 2$ , this one containing only crops (15 m). The top ranked model explaining *Apodemus sylvaticus* detection contained

solar altitude, proportion of artificial habitat, proportion of open habitat and proportion of forest habitat (Table 5). No other model was supported.

### ***Microtus agrestis***

The top ranked model explaining *Microtus agrestis* occupancy contained only the amount of built-up habitat (15 m) (Table 4). Four other models were within 2 of the top ranked models AIC<sub>c</sub>, with three containing the amount of built-up habitat (15 m), two including human population density, with the amount of transport infrastructure (800 m) and distance to port being included in one each. The top ranked detection model for *Microtus agrestis* included solar altitude, proportion of artificial habitat and proportion of forest as covariates (Table 6). Four other models had support, with solar altitude and proportion of forest being included in all, proportion of open and artificial habitat being included in two, and average distance to transport infrastructure being included in one (Table 5).

### ***Sorex araneus***

The top ranked model explaining *Sorex araneus* occupancy had only human population density as its predictor (Table 4). One other model was supported, this one including the distance to transport. The top ranked detection model for *Sorex araneus* contained solar altitude, proportion of open habitat, distance to built-up areas, and distance to transport (Table 5). One other model was supported, this one dropping distance to built-up areas.

### ***Sorex minutus***

The top ranked model for *Sorex minutus* contained the amount of forest (800 m) and pasture (800 m) as predictors (Table 4). One other model was supported, with the same predictors including the amount of built-up area (15 m). The top ranked detection model for *Sorex minutus* included solar altitude and the proportion of open habitat (Table 5). Four other models were supported, all of them including solar altitude, two including the proportion of open habitat, and one each including the proportion of forest habitat, distance to built-up areas, and distance to transport.

Table 4. Model selection results for occupancy models for the five species. Only models with  $\Delta AIC_c < 2$  were included.  $w$  denotes  $AIC_c$ -weights, while  $\Sigma w$  is the cumulative weights.

	Model	$AIC_c$	$\Delta AIC_c$	$w$	$\Sigma w$
<i>Crocidura russula</i>	Population + Forest (800 m)	819.22	0.00	0.12	0.12
	Distance to ocean + Population + Forest (800 m)	819.47	0.25	0.10	0.22
	Population	820.05	0.83	0.08	0.30
	Distance to ocean + Population	820.18	0.95	0.07	0.37
	Distance to ocean	820.54	1.32	0.06	0.43
	Distance to ocean + Distance to transport + Forest (800 m)	820.63	1.41	0.06	0.49
	Distance to ocean + Distance to transport + Population	820.78	1.56	0.05	0.55
	Distance to ocean + Forest (800 m)	820.80	1.58	0.05	0.60
	Distance to transport + Population + Forest (800 m)	820.88	1.66	0.05	0.65
	Distance to transport + Population	821.15	1.93	0.04	0.70
	Distance to port + Crops (15 m)	1941.95	0.00	0.46	0.46

<i>Apodemus sylvaticus</i>	Crops (15 m)	1942.97	1.02	0.28	0.74
<i>Microtus agrestis</i>	Built (15 m)	260.63	0.00	0.14	0.14
	Population + Built (15 m)	261.18	0.55	0.11	0.25
	Distance to port + Built (15 m)	261.50	0.87	0.09	0.34
	Built (15 m) + Transport (800 m)	261.90	1.27	0.07	0.41
	Population	262.45	1.83	0.06	0.47
<i>Sorex araneus</i>	Population	785.74	0.00	0.58	0.58
	Distance to transport + Population	786.69	0.95	0.36	0.93
<i>Sorex minutus</i>	Forest (800 m) + Pasture (800 m)	220.45	0.00	0.31	0.31
	Built (15 m) + Forest (800 m) + Forest (800 m)	221.46	1.02	0.19	0.50

Table 5. Overview of the top-ranked detection models for each study species. Only species with lower than 2  $\Delta AIC_C$

	Model	$AIC_C$	$\Delta AIC_C$	w	$\Sigma w$
<i>Crocidura russula</i>	Solar altitude + Artificial + Forest + Open	821.72	0.00	0.76	0.76

<i>Apodemus sylvaticus</i>	Solar altitude + Artificial + Forest + Open	1947.07	0.00	0.99	0.99
<i>Microtus agrestis</i>	Solar altitude + Forest + Open	265.49	0.00	0.40	0.40
<i>Sorex araneus</i>	Solar altitude + Distance to built-up + Distance to transport + Open	815.81	0.00	0.50	0.50
	Solar altitude + Distance to built-up + Distance to transport	816.68	0.86	0.33	0.83
<i>Sorex minutus</i>	Solar altitude + Open	228.84	0.00	0.27	0.27
	Solar altitude	230.72	1.88	0.10	0.37
	Solar altitude + Distance to built-up + Open	230.78	1.94	0.10	0.47
	Solar altitude + Distance to transport + Open	230.83	1.99	0.10	0.57

### 3.3 Model averaging results

No predictor had a significant effect on the occupancy of *Crocidura russula* (Fig. 7). Human population density had a negative effect on the occupancy of *Microtus agrestis* and *Sorex araneus*, and a positive effect on *Crocidura russula*, however, the effect overlapped 0 for both *Crocidura russula* and *Microtus agrestis*. Distance to the ocean had a negative effect on *Crocidura russula*, with a confidence interval barely including 0. The amount of crops (15 m) had a negative effect on *Apodemus sylvaticus* ( $\beta = -0.0246$ , CI = -0.0438 - -0.0053), and the amount of pasture (800 m) had a positive effect on *Sorex minutus* ( $\beta = 0.15$ , CI = 0.032 - 0.267)

Solar altitude had a negative effect on the detection probability for all species, with detection probabilities being higher during night-time and getting progressively lower during the day



(Fig. 8). The proportion of artificial habitat had a positive effect on the detection probability of *Crocidura russula* ( $\beta = 0.28$ , CI = 0.156 – 0.394) and a negative effect on *Apodemus sylvaticus* ( $\beta = -0.51$ , CI = -0.366 – -0.653), meaning that *Crocidura russula* was easier to detect when the sites were surrounded by higher proportions of artificial habitat while the opposite was true for *Apodemus sylvaticus*. Distance to transport and distance to built-up areas had a negative effect on the detection of *Sorex araneus*, indicating that the species were easier to detect at sites further away from transport and built-up areas. The proportion of forest habitats had a positive effect on the detection probability of *Apodemus sylvaticus* and *Crocidura russula*, and a negative effect on *Microtus agrestis* ( $\beta = 0.40$ , CI = -0.75 – -0.05 ).

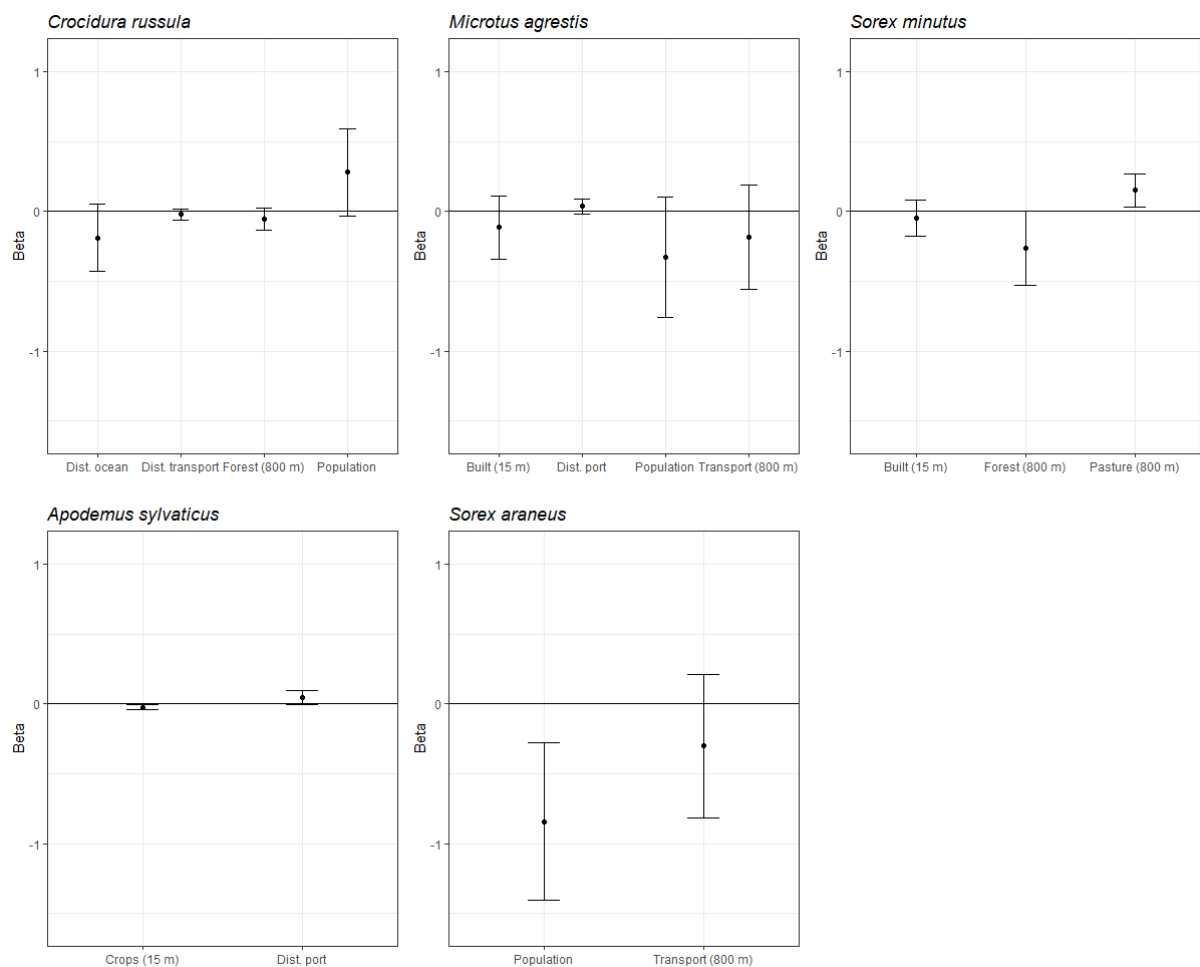


Figure 7. The model-averaged estimates covariate effects on occupancy probability for each species. The points represent the model-averaged means, and the error bars represent the 95 % confidence interval. A table of the estimates is shown in Table A2.

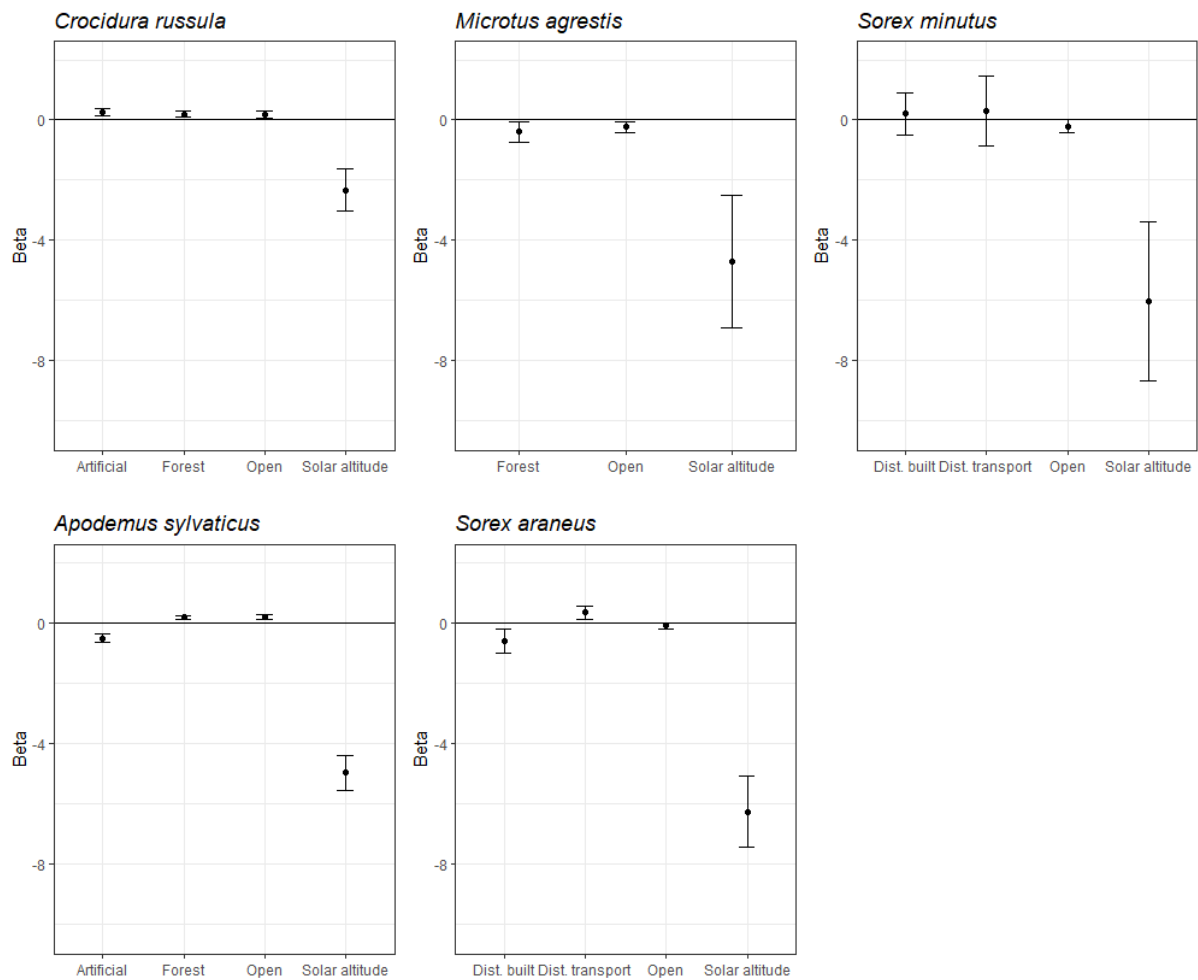


Figure 8. The model-averaged estimates of predictors on detection probability for each species. The points represent the model-averaged means, and the error bars represent the 95 % confidence interval. A table of the estimates is shown in Table A3.

### 3. 4 Effect of *Crocidura russula* on other species

The co-occupancy models did not reveal any significant effect of *Crocidura russula* on the occupancy of the other species. Similarly, the number of *Crocidura russula* observations did not have a significant effect on the number of observations for any of the other study species.

Table 7. The effect of *Crocidura russula* on the occupancy of the other study species. Results from the co-occupancy model.

	$\beta$	SE	P(> z )
<i>Apodemus sylvaticus</i>	0.743	0.717	0.301
<i>Microtus agrestis</i>	-0.111	0.892	0.901
<i>Sorex araneus</i>	0.273	0.654	0.677
<i>Sorex minutus</i>	-0.149	0.937	0.874

Table 8. Results of linear regression on the effect of *Crocidura russula* presence and activity on the activity of the other study species.

	Presence			Activity		
	$\beta$	SE	P(> t )	$\beta$	SE	P(> t )
<i>Apodemus sylvaticus</i>	-4.617	11.685	0.694	-0.0877	0.3494	0.802
<i>Microtus agrestis</i>	0.8504	0.9256	0.361	-0.0116	0.0278	0.677
<i>Sorex araneus</i>	-0.8692	2.4428	0.723	-0.0326	0.0730	0.656
<i>Sorex minutus</i>	0.7613	0.7866	0.336	-0.0116	0.0236	0.627

## 4. Discussion

Even though the greater white-toothed shrew (*Crocidura russula*) most likely is a recent invader, it is already common in the study area. *Crocidura russula* was first discovered in Norway in 2012 and has already reached comparable occupancy levels as native species such as *Microtus agrestis*, *Sorex araneus*, and *Sorex minutus*, while still being lower than the common *Apodemus sylvaticus*. Based on the occupancy estimate, *Crocidura russula* now covers an area of 154 km<sup>2</sup> (CI = 84 km<sup>2</sup> - 250 km<sup>2</sup>), which represents 24.8 % of the total study area. This suggests that *Crocidura russula* is well-established in the area and is able to propagate successfully. While estimating range expansion was not possible due to lack of multi-season data, this also suggests that *Crocidura russula* is spreading at a fast rate and is at least not completely constrained to its initial introduction point. *Crocidura russula* is also spreading fast in Ireland, where *Crocidura russula* has also been introduced (McDevitt et al., 2014). The expansion of *Crocidura russula* has also caused the displacement of *Sorex minutus* in the areas it inhabits (McDevitt et al., 2014), but this does not seem to be the case in the study area at present, as both species were present in close proximity and at the same sites.

*Crocidura russula* is known to be highly anthropophilic at its northern distribution edge (Favre et al., 1997), but human population density did not have a significant effect on occupancy in this study. Human population density may be an inadequate and too coarse estimate for the anthropogenic features *Crocidura russula* utilizes. More fine-scale covariates such as distance to gardens or residences could give a better estimate of the effect of human infrastructure on the occupancy probability of *Crocidura russula*. Interestingly, *Sorex araneus* and *Microtus agrestis* had a negative association with human population density, while the estimate for *Crocidura russula* was positive.

Distance to port was not a significant predictor of *Crocidura russula* occupancy and was not included in any of the top-ranking models. Stavanger port is the suspected point source, but this study did not find evidence to support this hypothesis. There are some possible explanations for this. *Crocidura russula* could have another point source, it could for example have arrived in a container shipped from Continental Europe by road. Since *Crocidura russula* can enter torpor (Nagel, 1977), it would be able to survive without food for the duration. Another possibility is that *Crocidura russula* has already spread far enough for the point source to no longer matter. Since the study area is located by the Atlantic Ocean

and far from the Swedish border, *Crocidura russula* is very likely to have had human help in spreading there. However, the shipment could have arrived at Stavanger port before being opened at its destination. In any case, finding a point source will probably be difficult.

*Crocidura russula* had the highest detection probability of all the studied species. This suggests that the survey design was adequate for detecting *Crocidura russula* and that the sample effort (mean = 2.16 days) was sufficient. The high detection probability could be caused by the fact that *Crocidura russula* is relatively social and not very territorial outside of the mating season (Cantoni, 1993; Genoud, 1985), and thus can achieve high population densities. Local abundance has a positive effect on detection probability (McCarthy et al., 2013), and the potentially higher densities of *Crocidura russula* could make it easier to detect than the native species in the study.

Identifying covariates that affect detection probabilities makes it possible to create better survey designs, which then gives us better and more accurate occupancy models and makes it easier to identify covariates that affect occupancy probabilities. For example, trapping sites can be placed in microhabitats that increase the likelihood of detection, such as those with open, artificial, or forest habitat for *Crocidura russula*, while maintaining a random or systematic site selection at the occupancy level. Another possibility is stratification, where all types of habitats are sampled, but prioritising habitats most likely to have high detection or occupancy probabilities.

This study was not able to identify a negative impact of *Crocidura russula* on native small mammals. The co-occupancy estimates were not significant, and the presence and activity of *Crocidura russula* did not significantly affect the activity of the other species. While this study was unable to detect an effect, it is still possible that *Crocidura russula* does have a negative impact on other small mammals. The data was limited, for example, *Sorex minutus* only occurred in eight sites, making it difficult to analyse the interaction between the species. It may also take some time before *Crocidura russula* has an impact on native species. Early growth might be exponential which is inherently slow at the start (Crooks, 2005). Another possibility is that since *Crocidura russula* is limited by temperature, it is unable to reach high enough population densities to pose a serious problem to native species. This could change with anthropogenic climate change, as air temperatures are predicted to increase and snow cover decrease in the area (Hanssen-Bauer et al., 2009; Krasting et al., 2013) potentially making new habitats available to *Crocidura russula* and increasing its negative impact.

While this study only used camera trapping data to model occupancy, integration of data from multiple survey methods could improve the predictive ability of models. While site-occupancy surveys, such as camera trapping, produces high-quality data containing both detections and non-detections, they are costly and seldom represent the full geographic range of the species (Koshkina et al., 2017). In contrast, opportunistic surveys such as citizen science reports are more likely to produce biased data, but often covers a larger area. Koshkina et al (2017) propose a way to combine both survey methods, with the integrated model showing superior predictive ability when tested on data for the Yellow-bellied glider (*Petaurus australis*). This could be a useful approach for future occupancy analyses for *Crocidura russula*.

Future studies should focus on estimating the spread of *Crocidura russula* and its effect on competing species. By utilizing a multi-season approach and expanding the study area, the range and spread of *Crocidura russula* could be estimated. Since *Crocidura russula* does not require much sampling effort to detect, more resources should instead be used to increase the number of sites, thus allowing us to analyse predictors of occupancy more accurately. Using occupancy models to test additional predictors could in turn allow us to disentangle what characterises sites occupied by *Crocidura russula*, thus making it easier to predict future expansion. Knowledge about what drives the expansion of *Crocidura russula* would also be beneficial when it comes to managing the problem. For example, if roads were found to have a positive effect on the spread of *Crocidura russula*, management efforts could focus on decreasing the attractiveness of roads as dispersal corridors. This could be done by manipulating vegetation at road verges, thus making it more difficult to travel alongside the roads. All in all, this study shows that *Crocidura russula* is established in the study area and seems likely to continue spreading.

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## Appendix

Table A1. Overview of the species detected during camera trapping, trapping, and confirmed reports.

Common name	Scientific name
American mink	<i>Mustela vison</i>
Brown rat	<i>Rattus norvegicus</i>
Common blackbird	<i>Turdus merula</i>
Common grasshopper warbler	<i>Locustella naevia</i>
Eurasian shrew	<i>Sorex araneus</i>
Common toad	<i>Bufo bufo</i>
Common whitethroat	<i>Sylvia communis</i>
Domestic cat	<i>Felis catus</i>
Dunnock	<i>Prunella modularis</i>

Eurasian magpie	<i>Pica pica</i>
Eurasian pygmy shrew	<i>Sorex minutus</i>
Eurasian water shrew	<i>Neomys fodiens</i>
Eurasian wren	<i>Troglodytes troglodytes</i>
European hedgehog	<i>Erinaceus europaeus</i>
European robin	<i>Erithacus rubecula</i>
European roe deer	<i>Capreolus capreolus</i>
Field vole	<i>Microtus agrestis</i>
Greater white-toothed shrew	<i>Crocidura russula</i>
Meadow pipit	<i>Anthus pratensis</i>
Song thrush	<i>Turdus philomelos</i>

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Table A2. Model-averaged parameter estimates for occupancy. Standard error and CI are unconditional. Predictors whose 95 % confidence interval did not overlap 0 are highlighted in **bold**.

	Predictor	$\beta$	CI
<i>Crocidura russula</i>	Population	0.2805	-0.0323 – 0.5933

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	Forest (800 m)	-0.0552	-0.1359 – 0.0255
	Distance to ocean	-0.1888	-0.4263 – 0.0499
	Distance to transport	-0.0212	-0.0609 – 0.0185
<hr/>			
<i>Apodemus sylvaticus</i>	<b>Crops (15 m)</b>	-0.0246	-0.0438 – -0.0053
	Distance to port	0.0458	-0.0053 – 0.0970
<hr/>			
<i>Microtus agrestis</i>	Built (15 m)	-0.1169	-0.3399 – 0.1060
	Population	-0.3291	-0.7591 – 0.1008
	Distance to port	0.0342	-0.0204 – 0.0888
	Transport (800 m)	-0.1874	-0.5601 – 0.1853
<hr/>			
<i>Sorex araneus</i>	<b>Population</b>	-0.8431	-1.4077 – -0.2785
	Transport (800 m)	-0.3025	-0.8159 – 0.2109
<hr/>			
<i>Sorex minutus</i>	<b>Pasture (800 m)</b>	0.1494	0.0315 – 0.2673
<hr/>			

Forest (800 m)	-0.2634	-0.5275 – 0.0007
Built (15 m)	-0.0478	-0.1774 – 0.0819

Table A3. Model-averaged parameter estimates for detection. Standard error and CI are unconditional. The intervals have a confidence level of 95 %. Predictors whose confidence intervals do not overlap with 0 are highlighted in **bold**.

	Predictor	$\beta$	CI
<i>Crocidura russula</i>	<b>Artificial</b>	0.2751	0.1560 – 0.3942
	<b>Forest</b>	0.1985	0.0904 – 0.3065
	<b>Open</b>	0.1916	0.0732 – 0.3099
	<b>Solar altitude</b>	-2.3254	-3.0266 – -1.6242
<i>Apodemus sylvaticus</i>	<b>Artificial</b>	-0.5096	-0.6532 – -0.3660
	<b>Forest</b>	0.1900	0.1211 – 0.2590
	<b>Open</b>	0.2044	0.1375 – 0.2712
	<b>Solar altitude</b>	-4.9869	-5.5513 – -4.4226
	<b>Forest</b>	-0.4011	-0.7495 – -0.0527

<i>Microtus agrestis</i>	<b>Open</b>	-0.2401	-0.4245 – -0.0558
	<b>Solar altitude</b>	-4.7075	-6.8964 – -2.5187
<hr/>			
<i>Sorex araneus</i>	<b>Distance to transport</b>	0.3419	0.1280 – 0.5558
	Open	-0.0886	-0.1872 – 0.0100
	<b>Distance to built</b>	-0.5973	-0.9856 – -0.2089
	<b>Solar altitude</b>	-6.2758	-7.4557 – -5.0959
<hr/>			
<i>Sorex minutus</i>	Open	-0.2153	-0.4398 – 0.0093
	Distance to built	0.2048	-0.4952 – 0.9047
	Distance to transport	0.3056	-0.8517 – 1.4630
	<b>Solar altitude</b>	-6.0400	-8.6925 – -3.3875
<hr/>			

Reference list



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