

Species-area relations and island distribution of carabid beetles (Coleoptera, Carabidae) on small islands off the coast of western Norway

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The study explores carabid beetle communities on small islands to assess distribution patterns in terms of stochastic and non-random mechanisms. The study was carried out on 14 small islands in Øygarden, an island archipelago 30 km north-west of Bergen, western Norway. The dominant vegetation was *Calluna* heath. Sampling was carried out with 83 pitfall traps operating continuously from 30 May to 14 November 1983. Log-linear regression was applied for analysing the data. The pitfall trapping yielded 29 species and 6139 specimens of ground beetles (Coleoptera, Carabidae). Island area was less significant than the habitat size in determining the species diversity. An island further away from the source area contained a higher proportion of species with the ability to fly than did islands close to the source area (i.e. nearest large island). Islands exposed to the actions of wind and waves were inhabited by species with adult hibernation. The immigration rate of *Carabus problematicus* Herbst, 1786 is probably very low, leading to a certain degree of genetic isolation, expressed by differences in size between islands. Carabid beetles from small islands off the coast of western Norway were non-randomly distributed according to habitat size and distance from source areas. Extreme areas such as small islands alter carabid beetle communities in a profound way.

Key words: Carabid beetles, Carabidae, hibernation strategies, dispersal, genetic isolation, small islands

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INTRODUCTION

The basic concepts of island biogeography presented by MacArthur & Wilson (1967) have been tested for a number of organisms, e.g. mammals (Lomolino 1984) and birds (Brown & Dinsmore 1988). The general theory put forward by MacArthur and Wilson (1967) was an important step forward in the theory of island

biogeography and has been recently extended by more refined theories (Lomolino 2000). However, empirical observations and testable hypotheses are still needed to fill in the gaps.

Successful colonization of islands is dependent of a range of factors, of which dispersal abilities and habitat availability are among the most important ones. Both aspects have received much attention in

the case of carabid beetles (den Boer 1970, 1980, 1990, Hatteland et al. 2005a), also in the process of island colonization (Kotze & Niemelä 2002, Niemelä 1988, Niemelä et al. 1988, Ås 1984). It is obvious that flight ability is advantageous when considering dispersal abilities, but it is also well known that insects on remote islands have lost their ability to fly and have become apterous (Darlington 1943, Darwin 1859). We investigate whether the advantage of flight ability leads to a higher frequency of carabids with flight ability further away from the source area. Also, we deal more thoroughly with the question of flight ability, assuming that the possession of wings does not necessarily mean a high degree of flight ability. Previous studies have revealed the importance of examining the length of the wings in order to predict the flight ability (den Boer 1980). Moreover, the possession of fully developed flight wings in carabids varies geographically (Bangsholt 1983, Lindroth 1949).

The ecological stability of an island is thought to be related to its size. Paarmann (1979) and Luff (1993) argued that the hibernation strategy of carabid beetles is connected to the stability of the habitat, while Lindroth (1949), Thiele (1977) and Andersen (1984) related the hibernation strategy to temperature. They all found that the oceanic climate in western Norway favours larval hibernation, a finding that is also supported by studies from western (Hatteland in prep.) and central Norway (Hatteland et al. 2005b). According to Paarmann (1979) one would expect adult hibernators on small, exposed and thus unstable habitats. In the present study we test whether this is true for small islands off the coast of western Norway.

The distribution of species on islands is in the sense of MacArthur & Wilson (1967) a stochastic event. The opposite view is held by Lack (cited in Williamson 1981): the distribution is dependent on the ecology of each individual species. Ranta & Ås (1982) found that carabids colonized habitat islands non-randomly. Furthermore, Niemelä et al. (1987) found a "mosaic distribution" among several species, being abundant on some islands,

but scarce or absent on others. An importation question in the present study was to find if the present distribution of carabid species in western Norway follows stochastic or non-random distribution patterns.

MATERIAL AND METHODS

Study area

The study was carried out at Øygarden, an island archipelago 30 km north-west of Bergen, western Norway (Figure 1). The area consists of a total of 550 islands and about a few hundred skerries. The islands studied are all on the west part of Øygarden, exposed to the North Sea. The climate is oceanic, with mean temperatures for August and February of 14.1 °C and 1.8 °C, respectively.

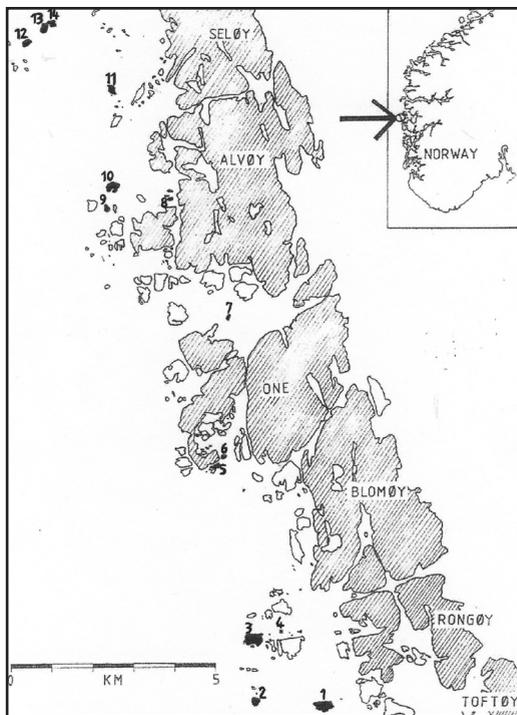


Figure 1. The study area. The islands studied are shaded.

The prevailing winds are south-westerly and north-westerly. Mean annual precipitation is 1200 mm. The carabid beetles were sampled from 14 islands and skerries ranging in size from 0.24 to 10.6 ha (Table 1). All these islands are characterized by

Table 1. Data on area, distance from source area, number of traps and vegetation for the 14 islands in the study.

Island number	Total area (ha)	Degree of veg. Cover (%)	Veg. Area (ha)	Distance (km)	No. traps
1	7.13	7	0.54	0.60	10
2	2.87	5	0.14	2.11	10
3	10.64	31	3.31	1.42	10
4	0.24	3	0.01	1.08	3
5	1.69	4	0.07	0.04	5
6	1.05	3	0.03	0.04	5
7	0.56	50	0.28	0.21	5
8	0.67	25	0.17	0.11	5
9	2.00	26	0.51	0.50	5
10	5.90	22	1.32	0.75	5
11	2.94	0	0.07	1.04	5
12	3.05	4	0.17	2.71	5
13	3.71	14	0.51	2.21	5
14	2.24	24	0.54	2.08	5

a discontinuous and patchy vegetation cover and most of them are bare rock. The larger islands, 3 and 10, have a more continuous vegetation cover, consisting mostly of *Calluna vulgaris* heath. The other six islands consist of varied vegetation, but most of them are covered with grasses and herbs. All the islands with a vegetated area larger than 1.6 ha, apart from island 14, have been used as grazing areas for sheep over many generations. This has modified the vegetation and prevented the *Calluna* heath from growing to full height.

The size of the islands, the size of the vegetated area and the degree of vegetation cover were calculated from aerial photographs. The distance to source area was defined as the distance to the nearest large island (shaded in Figure 1).

Sampling and analysing methods

Pitfall traps were placed approximately 4 m apart, 5 in a row (except island 4 where 3 traps were placed). One or two rows of traps were placed on each island, dependent on the size of the island (Table 1). The different number of traps was chosen for practical reasons. The traps were glass

jars with a slightly constricted opening, an inner diameter of 56 mm and a depth of 116 mm. A 4 % formalin solution was used. The traps were protected from rain and bird predation by a metal roof, 11x11 cm. The traps were operated from 30 May 1983 to 14 November and emptied once during the trapping.

Wing lengths are given as relative wing length, which is the length of the wing divided by the length of the elytra. Head width of *Carabus problematicus* was also measured due to a seemingly high degree of variation between islands suggesting habitat effects and genetic isolation.

Statistical methods used are found in (Sokal & Rohlf 1981). Both the species-area and the species-habitat regression are on a log-linear regression expressed by the equation $S = K + Z \log A$, which is commonly expressed as a power function.

Table 2. The number of carabid beetles caught at the 14 islands and skerries. M = macropterous, D = dimorphic and B = brachypterous. I = hibernation as imago, L = hibernation as larvae. Hibernation strategies are according to Thiele (1977) and Lindroth (1985, 1986).

SPECIES / ISLAND NUMBER	Type of wings	Wing length (mm)	Hibernation strategy														Total		
			1	2	3	4	5	6	7	8	9	10	11	12	13	14			
<i>Amara aulica</i> (Panzer)	M	1.4-1.5	L	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	2
<i>A. communis</i> (Panzer)	M	1.3	M	2	1	-	-	-	-	-	-	10	3	-	-	23	-	2	67
<i>A. familiaris</i> (Duitschmid)	M	1.3-1.5	I	4	1	-	-	-	-	-	-	-	-	-	2	-	-	7	
<i>A. lunicollis</i> Schiödte	M	1.4	I	1	-	-	-	-	-	-	-	-	3	1	-	-	-	17	
<i>A. ovata</i> (Fabricius)	M	1.4	I	43	-	-	78	4	2	-	-	-	-	-	51	172	2	352	
<i>Bembidion tetracolum</i> Say	M	1.4	I	-	-	-	2	-	-	-	-	-	-	-	-	-	-	2	
<i>Calathus fuscipes</i> (Goeze)	B	0.4 and 1.5	L	-	-	40	-	-	-	-	-	-	-	-	-	-	-	40	
<i>C. melanocephalus</i> (L.)	B	0.4 and 1.5	L	-	2	-	-	-	-	-	-	-	-	-	-	-	-	13	
<i>Carabus problematicus</i> Herbst	D	0.7 and 1.4-1.5	L	-	135	-	-	12	-	-	-	62	142	-	-	-	44	735	
<i>Clivina rorosa</i> (L.)	D	0.7 and 1.4-1.5	L	-	-	-	-	-	-	-	-	-	-	-	-	5	-	5	
<i>Cychinus caraboides</i> (L.)	B	0.4	L	-	4	-	-	-	-	-	-	-	15	-	-	-	-	19	
<i>Dyschirius globosus</i> (Herbst)	M	0.4	M	-	-	31	-	-	-	-	-	1	-	-	-	-	-	33	
<i>Heptapus latus</i> (L.)	M	1.2-1.5	I/L	-	8	-	-	-	-	-	-	1	8	-	-	-	-	23	
<i>Loricera pilicornis</i> (Fabricius)	M	1.5	L	7	47	-	-	-	-	-	-	-	-	-	19	-	-	73	
<i>Nebria salina</i> Famm.	M	1.4-1.5	L	107	107	392	-	59	-	319	112	93	119	-	578	101	24	2011	
<i>Notophilus aquaticus</i> (L.)	M	0.2-0.3	I	-	6	-	-	5	-	-	-	-	-	-	-	-	-	11	
<i>N. biguttatus</i> (Fabricius)	D	0.4 and 1.3	I	-	-	-	-	-	-	-	-	-	-	-	-	-	4	4	
<i>Olistophus rotundatus</i> (Paykull)	M	0.2	L	5	2	16	-	-	-	5	-	-	122	85	16	21	-	11	
<i>Patrobus assimilis</i> Chaudoir	B	-	L	-	-	-	-	-	-	-	13	-	-	-	-	-	-	13	
<i>P. atronulus</i> (Strom)	B	-	L	6	105	2	-	16	11	11	23	71	5	-	-	-	-	250	
<i>Pterostichus diligens</i> (Sturm)	M	0.2	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	
<i>P. melanarius</i> (Illiger)	B	-	L	-	-	-	-	-	-	6	-	-	-	-	-	-	-	6	
<i>P. niger</i> (Schaller)	M	1.1	L	10	-	4	-	1	-	24	1	-	68	-	-	3	15	116	
<i>P. nigrita</i> (Paykull)	M	0.9-1.4	I	-	-	-	-	-	-	2	-	4	-	-	-	-	-	28	
<i>P. oblongopunctatus</i> (Fabricius)	M	0.9-1.1	I	-	18	-	-	-	-	-	-	-	1	-	-	-	-	19	
<i>P. strenuus</i> (Panzer)	M	0.2-0.5	L	212	1	1	353	407	106	63	46	172	60	283	114	2	8	1828	
<i>P. versicolor</i> (Sturm)	M	0.9-1.2	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	
<i>Trechus obtusus</i> Erichson	B	-	L	-	-	-	-	-	-	-	-	-	-	-	-	15	-	15	
<i>T. secalis</i> (Paykull)	B	-	L	-	-	-	-	-	-	-	126	1	-	-	-	-	-	127	
Total species				8	9	16	4	7	3	16	10	8	13	2	8	5	8	29	
Total individuals				356	312	647	464	504	119	790	424	370	652	334	928	109	130	6139	

RESULTS

A total of 29 species of Carabidae (Coleoptera) were trapped and the total yield was 6139 specimens (Table 2).

The species-area regression is not significant ($p > 0.1$). The Z-value in the species-area equation is very small compared with the theoretical value expected (Gilbert 1980). The species-habitat area relationship is however significant ($p=0.00582$), and the Z-value obtained is very close to the theoretical value (Figure 2).

The range of the relative wing lengths of the 21 species that are referred to as either macropterous or dimorphic (Lindroth 1985, 1986, Thiele 1977) are given in Table 2. The remaining eight species are exclusively brachypterous. The proportion of species with flight ability is positively correlated with the distance to the source area (Figure 3).

The species with larval or adult hibernation are given in Table 2; the latter is significantly inversely correlated with the degree of vegetation cover in terms of species as well as individuals (Figure 4). The two most exposed islands, 4 and 10, are exclusively inhabited by adult hibernators. These are more or less inundated by waves during winter storms. The second two most exposed islands, 5 and 6, were inhabited by a proportion of 86 % and 100 % adult hibernators, respectively.

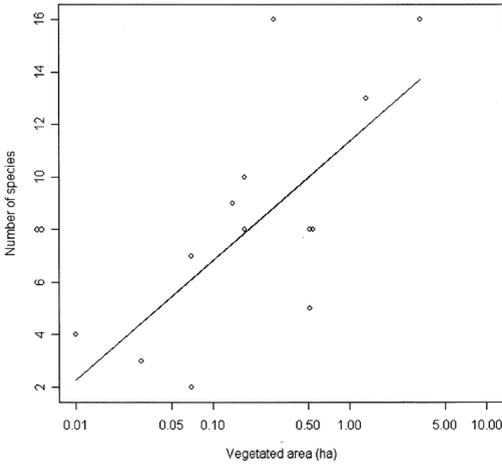


Figure 2. The species-area regression using the vegetated or habitat area. The curve is expressed as $S = 11.363 + 4.545 \log A$.

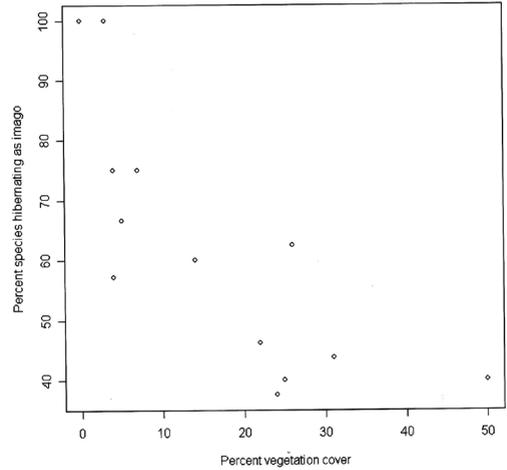


Figure 4. The relation between imaginal hibernation given in percent and exposure, expressed as relative vegetation cover. Spearman's Rank Correlation, $N = 14$, $r_s = -0.821$, $p < 0.001$.

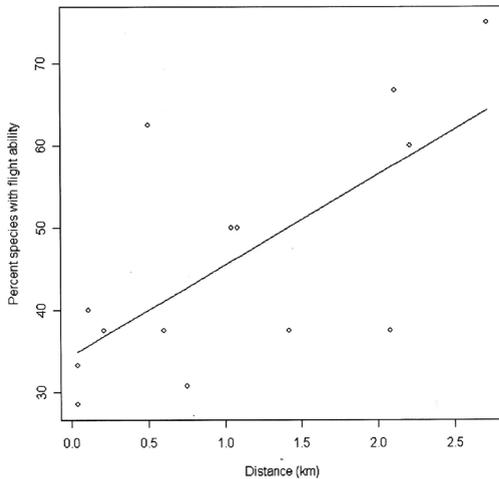


Figure 3. The relation between the fraction of species with flight ability and the distance from source area. Spearman's Rank Correlation, $N = 14$, $r_s = 0.598$, $p < 0.02$.

The species had an uneven distribution (Table 2). *Amara ovata* (Fabricius, 1792) was only found on the smallest islands, islands with gull colonies and islands heavily exposed by wind and waves. *Amara lunicollis* Schiødte, 1837, *Carabus problematicus* Herbst, 1786, *Harpalus latus* (L., 1758), *Pterostichus niger* (Schaller, 1783) and *P. nigrita* (Paykull, 1790) are all species that

are found on the larger islands with grasses and *Calluna* heath. The species are non-randomly distributed according to the size of the beetles. The larger species are found in the larger habitat patches, and this association is significantly correlated (Spearman Rank Correlation Test, $N=29$, $r=0.432$ and $p<0.05$).

The head widths of *C. problematicus* on the five islands on which it occurs are given in Table 3. Head widths of specimens from island 8 and 14 are significantly different from those of island 3, 7 and 10 (Analysis of Variance performed on males: $p<0.001$ and females: $p<<0.001$).

DISCUSSION

It is clear that the area of a physical island in this study can be of little importance in predicting the number of species. The obvious reason for this is that the size of the actual habitat is the limiting factor to the number of species. In our study, where the difference between island size and habitat size varies so much, what we have actually studied is "islands on islands", i.e. habitat patches. Obviously, the islands consist of a few and specialised microhabitats, which probably

Table 3. The mean head width of *Carabus problematicus* on five islands.

Island number	MALES			FEMALES		
	Mean head width (mm)	S.D.	N	Mean head width (mm)	S.D.	N
3	4.07	0.17	20	4.30	0.10	20
7	4.08	0.17	20	4.30	0.14	20
8	3.94	0.13	20	4.00	0.19	20
10	4.09	0.11	20	4.29	0.17	20
14	4.19	0.11	19	4.42	0.12	20

affect the colonization of many carabid beetles. This is especially true for the larger species. A large carabid has a large home range (Grüm 1983), perhaps larger than the habitat patches available on the studied islands. According to these trends, MacArthur and Wilson's (1967) prediction of random distribution is not valid. In addition, large carabid species are mostly brachypterous meaning that the immigration rate is very low in physically isolated islands. The most abundant large species in our study, *Carabus problematicus*, may be genetically isolated on small islands (8 and 14) according to our data (Table 3). One of these islands is only 0.11 km from the source area, which means that the immigration rate of this species is extremely low. This may also be the case with other flightless carabids in this study area. In general, flightless beetles like *Carabus* spp. are excellent model-species in monitoring genetic differentiation within and between species in fragmented habitats (Kamer et al. 2005). However, the size differences in *C. problematicus* found in the present study might also be habitat related.

Based on den Boer (1980) we have drawn the assumption that the relative wing length ought to be at least 1.2 mm to enable the carabid beetle to fly. All the macropterous species that have been caught in window traps by den Boer (1980) have in our study a relative wing length of 1.3 mm or more. In addition, the three species with a relative wing length less than 1.2 mm; *Pterostichus niger*, *P. oblongopunctatus* (Fabricius, 1787) and *P. versicolor* (Sturm, 1824) have hardly ever been caught in window traps. The thirteen species with relative wing lengths of 1.3 mm and more are in

this study considered to possess potential flight ability. The correlation between the proportion of species with flight ability and distance to source area (Figure 4) indicates that species with flight ability have a higher rate of immigration on physical islands than species without flight ability. This may seem contradictory to the findings of Ås (1984), but his islands were as much as 40 km away from the source area. Other studies dealing with dispersal abilities and islands supports our results (Kotze & Niemelä 2002, Ulrich & Zalewski 2002). Our findings support the idea that carabids are able to fly a distance of a few kilometres and weather conditions suitable for flight (van Huizen 1979) frequently occur in the study area.

The inverse correlation between the proportion of adult hibernation and the vegetation cover suggests that islands with a small and discontinuous vegetated area favour beetles with adult hibernation. Moreover, the islands in the present study with a vegetation cover of 5% or less consisted of herbaceous plants. These are decomposed during winter, which means that during winter there is no vegetation shelter, making the microclimate less favourable. The stability of habitats seems therefore to be the most important issue in extreme areas like small islands, being heavily exposed to wind, waves and salt-water spray. This is the opposite of studies from inland areas of western and central Norway, where larval hibernators were most numerous as to species-diversity and abundance (Hatteland et al. 2005a, Waage 1984). The eggs, larvae and pupae of carabids are known to be more sensitive to changes in moisture than the adult beetle (Luff 2005, Thiele 1977). Larsson (1939) concluded that

larval hibernators prefer habitats well protected against climatic fluctuations in the microhabitat. In addition, starvation and cannibalism are important mortality factors to newly-hatched larvae (Luff 2005). Nelemans (1989) concluded that mortality of the pre-imaginal stages was the most influential factor affecting population fluctuations of the large sized beetle *Nebria brevicollis* (Fabricius, 1792). Furthermore, the potential growth rate of older larvae may be limited by food availability. These biotic factors may be more important in small habitat patches than larger patches, as both direct and indirect intraspecific competition may increase quickly as the population increases.

The present study clearly shows the importance of habitat patches and migration. It also shows that extreme conditions, like small islands, can alter the species assemblages in a profound way.

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