# THE UNDEREXPLOITED POTENTIAL OF BIRD CENSUSES IN INSULAR ECOLOGY

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ABSTRACT.—Studies of insular ecology usually focus on the species composition of island communities, but using census data can lead to many novel insights and ways to look at island communities. One-visit censuses, with the possibility of covering a much larger number of islands per unit effort, may often be superior to more accurate but time consuming methods. Using empirical data from land bird communities in the Åland archipelago, we discuss the number of species on islands, species-abundnace distributions, and colonizing strategies, emphasizing methodological aspects.

Both empirical tests and several theoretical arguments support the conclusion that 80% or more of the species breeding on an island are observed in a one-visit census. The species missed are many of the rarities, but one-visit censuses often include non-territorial visitors. One-visit censuses can also be used for examining the species-abundnace distribution, which may give rise to interesting biological hypotheses. Quantitative data allow us to construct density-based *prevalence functions,* introduced here, instead of examining incidence functions based on presence-absence data. Prevalence functions and their annual variability lead to meaningful biological hypotheses about insular communities.

The paradigm of island biogeography (MacArthur and Wilson 1967) has attracted ecologists to study the species composition of insular communities; as a result, species-area curves, estimates of species turnover, and incidence functions have been derived (e.g., Diamond 1975a, Diamond and May 1976, Wilcox 1980), but substantial controversy has emerged as regards the biological interpretation and even reality of many patterns (e.g., Simberloff 1976, 1978b; Connor and McCoy 1979; Connor and Simberloff 1979; Gilbert 1980).

The basic problem in insular ecology is to understand the relative importance of different factors structuring island communities. There is no compelling reason why examining species lists should be the only, or even the dominant, method in studying island bird communities, for many relevant tests require quantitative data. Indeed, we argue here that censuses of island birds provide a remarkable potential that has not been exploited by more than a handful of ornithologists, such as: Blondel (1979) and Ferry et al. (1976) studying Corsica; Emlen (1977b) studying the Bahamas; Ricklefs and Cox (1978) studying taxon cycles in the West Indies; and Nilsson (1977a) studying bird communities on small islands in a Swedish lake.

Our emphasis here will be on methodological aspects rather than on final results, although it seems impossible to us to discuss methods without reference to the particular problems studied. As will be evident from our discussion, one-visit censuses are useful in many practical situations. This is surprising and may seem outra-geous at first sight, but we argue that restricting the attention of insular ecologists to species lists makes it impossible to understand many real and interesting patterns in insular communities; it is therefore not a basic requirement that the census method used should be able to produce a complete species list. Our empirical data come primarily from a study in 1975–80 of land bird communities in the Åland archipelago, SW Finland; for additional data, see Haila et al. (1979, 1980a), Haila and Järvinen (1980) and Järvinen and Väisänen (1980).

## THE NUMBER OF SPECIES ON ISLANDS

To generate a complete list of bird species breeding on an island certainly requires a long period of intensive surveying. A mapping census based on 8–12 visits may be a good substitute, even if the data do not give positive evidence of breeding. But censuses based on one or a few visits can also be useful, athough the results are less accurate than mapping or long-period surveys. Both direct tests and theoretical arguments support this claim.

### DIRECT EMPIRICAL TESTS

We have studied land bird densities on more than 50 islands in the Åland archipelago in one or several breeding seasons using primarily censuses based on one visit. As one of the basic characteristics of insular communities is the number of species present, several tests have been conducted to find out the degree of completeness of our species lists.

The island Gåsholmen (about 14 ha) was censused in 1980, and the results were compared with a mapping census of the same island taken in the same year (Y. Haila and S. Kuusela, unpubl. data). The results (Table 1) can be summarized as follows. Of the 19 species judged to be territorial on the basis of mapping, 17 (89%)

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TABLE 1

RESULTS OF MAPPING COMPARED WITH RESULTS OF A ONE-VISIT CENSUS ON GÅSHOLMEN (14 HA) IN 1980

| Species | Mapping (territories) | One-visit (pairs) |
|---|---|---|
| Wryneck (*Jynx torquilla*) | 1 | 1 |
| White Wagtail (*Motacilla alba*) | 3 | 2 |
| Robin (*Erithacus rubecula*) | 3 | 2 |
| Thrush Nightingale (*Luscinia luscinia*) | 1 | 1 |
| Wheater (*Oenanthe oenanthe*) | 2 | 1 |
| Blackbird (*Turdus merula*) | 3 | 1 |
| Redwing (*T. iliacus*) | 4 | 3 |
| Icterine Warbler (*Hippolais icterina*) | — | 1 |
| Lesser Whitethroat (*Sylvia curruca*) | 2 | 1 |
| Whitethroat (*S. communis*) | 1 | 1 |
| Garden Warbler (*S. borin*) | 1 | 1 |
| Willow Warbler (*Phylloscopus trochilus*) | 3 | 4 |
| Goldcrest (*Regulus regulus*) | 1 | — |
| Spotted Flycatcher (*Muscicapa striata*) | 2 | 2 |
| Willow Tit (*Parus montanus*) | 3 | — |
| Blue Tit (*P. caruleus*) | 1 | 1 |
| Great Tit (*P. major*) | — | 1 |
| Red-backed Shrike (*Lanius collurio*) | — | 1 |
| Hooded Crow (*Corvus corone*) | — | 1[a] |
| Starling (*Sturnus vulgaris*) | 3 | 2 |
| Chaffinch (*Fringilla coelebs*) | 20 | 15 |
| Greenfinch (*Carduelis chloris*) | 1 | 1 |
| Yellowhammer (*Emberiza citrinella*) | 1 | 1 |
| Total | 56 | 39 + 5 non-territorial |

[a] Observed to be a visitor from a neighboring island.

were observed in the one-visit census; 70% of the territorial males were observed in the single test census. In addition, the one-visit census revealed five non-territorial birds, including four species not accepted as territorial in the mapping. The non-territorial birds were presumably visitors from nearby islands lying no farther than about 100 m away (this was directly confirmed for one non-territorial species).

In another test (Y. Haila and S. Kuusela, unpubl. data.), Bockholmen, an island of 38 ha, was mapped and the results compared with a line transect of 800 m running from one end of the island to the other. Mapping revealed 33 territorial species, and the transect, covering not more than 40% of the island, included 26 of them. In addition, four of the seven missing species were observed during the census, but outside the transect belt. The one-visit census thus revealed 91% of the territorial species.

Finally, we report census results from two larger islands. Ulversö (almost 6 km²) was surveyed during a period extending from late May to early July 1976, and we could thus establish the list of territorial land bird species with high accuracy; the species were breeders or sometimes probably single males. A transect census covering about 20% of the island revealed 53

species, or 84% of the total of 63 species. Slightly better results were obtained in 1979, but the total list may have been incomplete owing to a less efficient survey in that year. Transect censuses were also made on the "mainland" of Åland, which is an island of 970 km². A mere 214 km of transects, covering about 5% of the area, included 102 species, or 85% of the 120 species present (Haila et al. 1979).

Of course, the species missed in one-visit censuses are not a random sample from the actual community, but are usually species having very small populations. In the tests reported here (excluding those made on Ulversö and Åland, for which the relevant data are lacking), no species with four or more pairs was missed. Similarly, the results of one-visit censuses generally include visitors from surrounding areas, but they also are not a random subset of the species. In our tests, only one of the visitors had more than a single pair in the census.

## THEORY

While empirical tests are necessary, they cannot be repeated on every island. We observed empirically that typical one-visit censuses capture 85–90% of the territorial species on islands of different sizes, but there are theoretical rea-

sons for believing that this result is fairly general. Assume that: (1) Island bird communities have species-abundance distributions similar to those in mainland communities; (2) observation efficiency is similar on islands and on the mainland, usually 45–75% of the territorial pairs being observed on one visit (for data, see the compilation of Järvinen 1978b); and (3) a bird census can be approximated as a multinomial process (see Järvinen and Lokki 1978).

Simulations based on these assumptions and actual bird census data then show (Järvinen and Sammalisto 1973, Järvinen and Lokki 1978) that 80–100% of the species will be observed on a single visit. In general, the most convenient approach here would be rarefaction (e.g., Heck et al. 1975, Simberloff 1979), because that method gives directly the expected numbers of species in random samples from the actual community.

As density compensation is said to occur in many island bird communities, it is not clear how realistic our assumption (1) is, and it is also doubtful whether multinomiality can be regarded as a sufficiently realistic postulate (Järvinen and Lokki 1978, Kouki and Järvinen 1980).

The above assumptions can also be used to illustrate why the errors in species lists should indeed occur among the rare species. In consequence, what is gained by increasing the numbers of visits to an island is improved accuracy in recording the rare species in the island community.

An entirely different approach is to assume, following Preston (1962; see also May 1975), that assumption (1) is: the species-abundance distribution of insular communities is lognormal (for data, see below).

Without *any* assumptions on census efficiency, the effects of the incompleteness of the census on the species list can be analyzed, deriving maximum-likelihood estimates for the proportion of missing species on the basis of the theory of truncated lognormal distribution (Cohen 1961, Pielou 1975). In our censuses in 1976, 16 islands were surveyed completely. Data (numbers of pairs in each species observed in the one-visit censuses) for five larger ones among them gave the results in Table 2. For smaller islands, the estimates were usually smaller, but we doubt the validity of assumption (1) in these cases. The examination of our census data indicated that the assumption was valid in the above cases, although the sample sizes were not large enough to reveal other than gross deviations.

Finally, we may examine the theory of random sampling from communities having a specified species-abundance distribution (May 1975: 105–106, and related appendices) or the results of rarefaction as applied to bird census data

TABLE 2
NUMBER OF SPECIES OBSERVED ON FIVE ISLANDS WITH AN ESTIMATE OF PROPORTION OF PAIRS NOT OBSERVED

| Island | Species | Maximum-likelihood estimate of proportion not observed |
|---|---|---|
| Gåsholmen (14 ha) | 19 | 15% |
| Foderholmen (7 ha) | 17 | 15% |
| Klobban (8 ha) | 6 | 9% |
| Äskholm (3 ha) | 8 | 4% |
| Börkholm (5 ha) | 10 | 4% |

(Engstrom 1981, James and Rathbun MS). Without going into details, all results indicate that a random sample of 50% from the community gives most of the species, and very rarely will more than 20% of the species be missing.

We notice the following implications for island ecology:

(1) Omitting 10–20% of the species has little effect on species-area curves. In particular, if the best fit is a power function ($S = CA^z$, where $S$ = number of species, $A$ = area and $C$ and $z$ are fitted constants), omitting 10–20% of the species only depresses $C$ by the same percentage and somewhat increases the error variance. Of course, if the percentage of species missed differs on different-sized islands, the problem is more serious.

(2) Species turnover is heavily affected by the immigrations and extinctions of small populations (Jones and Diamond 1976, Järvinen, In press). One-visit censuses cannot indicate anything but striking differences in species turnover because of numerous cases of "pseudo-turnover" (Lynch and Johnson 1974). Instead, quantifying numerical changes in all populations, called individual turnover by Järvinen (1978c), is possible. The turnover of species is just one aspect of the dynamic behavior of insular communities, and there is no reason why serious attempts should not be made to understand and examine patterns of quantitative population changes on islands.

(3) One-visit censuses do not give exact presence-absence lists of species, and therefore it is impossible to examine whether a certain species combination really does not occur in the archipelago or whether it is just missing owing to inadequate sampling. Again, we emphasize that studying quantitative patterns in the coexistence of possible competing species could often be a much more fruitful strategy than examining species lists. Besides, it is not clear that missing
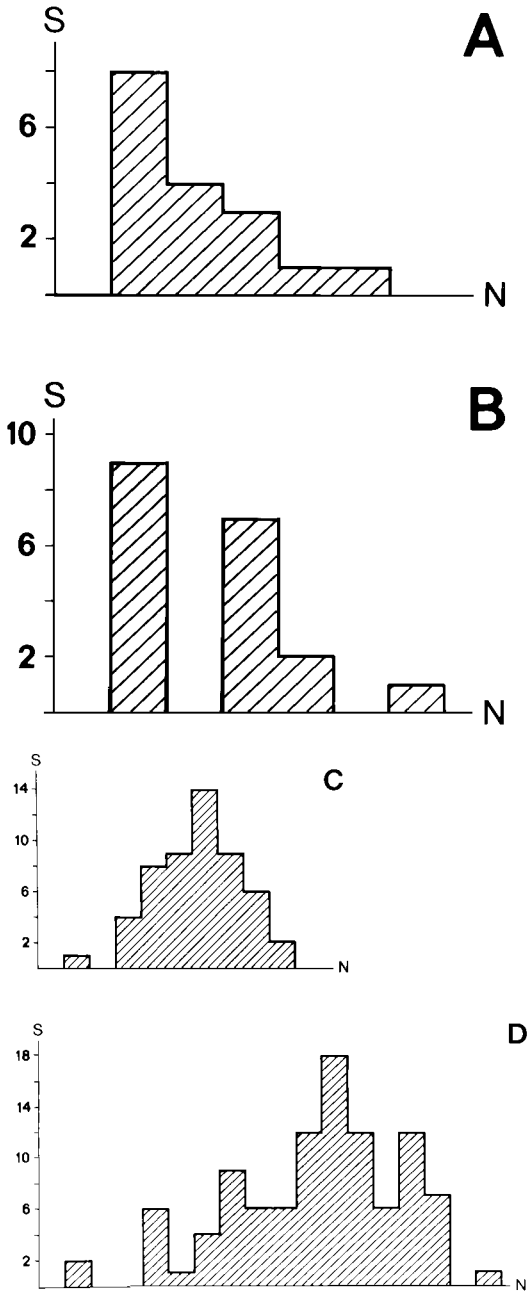
FIGURE 1. Species-abundance distributions on four islands in the Åland archipelago: A. Foderholmen (7 ha), B. Gåsholmen (14 ha), C. Ulversö (5.8 km²), and D. the mainland of Åland (970 km²). The number of pairs (N) is expressed on a logarithmic scale (base 2). D based on data from Haila et al. (1979); A–C our unpublished data.

combinations are particularly indicative of interspecific interactions.

(4) An important property of one-visit censuses is that they do not require an inordinate amount of time. While we readily acknowledge that absolutely accurate species lists are essential in studying certain problems of insular ecology and that more accurate census data are necessary for the solution of other problems, standardized one-visit censuses allow, for example, studying larger numbers of islands or repeating the census work more easily in several successive seasons in order to examine annual quantitative variability simultaneously in many insular communities. Of course, census work should be standardized as carefully as possible (for a review, see Berthold 1976). The important point is that the scope of questions can be broadened significantly if quantitative bird censuses are applied to insular ecology; the dynamic equilibrium model of MacArthur and Wilson (1967), whatever its merits and demerits, certainly does not exhaust all interesting island patterns.

Next we discuss the applicability of quantitative data to two central problems of insular ecology: species-abundance distributions and colonizing strategies.

## SPECIES-ABUNDANCE DISTRIBUTIONS

It is well-known (Preston 1962, MacArthur and Wilson 1967, May 1975) that if the species-abundance distributions on different islands are lognormal, the relationship between area and the number of species can be well approximated by a power function, assuming that densities do not vary with island size. What has usually been done is that the available data on the numbers of species and area have been fitted with a power function, without even examining other alternatives (see Connor and McCoy 1979), and the resulting fit has then been interpreted in terms of the prevailing paradigm. This is, however, unjustified (Connor and McCoy 1979, Gilbert 1980).

One important role for censuses is obviously that they can provide solid data for testing the basic premise of lognormality (Preston 1962). As full data will be published elsewhere, only examples (Fig. 1) are given here. As visual inspection indicates, the small islands usually have species-abundance distributions resembling the log-series model, but the distribution approaches lognormality as island size increases. Notice, however, that sample sizes per island are too small to discriminate effectively between various alternatives. We do not discuss the smallest islands here, but make a brief comment on the fact that the species-abundance distributions of the larger islands seem to be lognor-

mal except that they tend to be skewed to the left. This is interesting, because skewness constitutes a deviation from lognormality, which, according to May (1975), might be expected to be the rule. We give one possible explanation here, in order to show that quantitative data may broaden the scope of insular ecology. However, the following should not be interpreted as a final statement, because we have not given a rigorous statistical demonstration of our premise that skewness to the left is typical.

Suppose that skewness to the left is validly established as a typical pattern in the archipelago we have studied. In other words, there is a somewhat higher number of very small populations than May's (1975) statistical and probabilistic arguments would lead us to expect. An obvious hypothesis would be that the islands we have studied are actually not isolated from the standpoint of bird dispersal, but the birds use the whole archipelago more or less as a unit. Therefore, many of the islands may support very small populations that are not themselves self-sustaining but are a portion of a larger self-sustaining population in the archipelago and the nearby mainland. This idea can be tested on the basis of census data, if they are available. For example, if the whole archipelago is a unit, with no problems of dispersal between the islands, population increases on the islands occupied may be expected to lead to colonizations of new islands, and vice versa. This idea can also be applied to the Åland archipelago in its entirety, for it seems to be part of the mainland for many North European bird populations (Haila et al. 1979). An obvious alternative hypothesis, not supported by the data (Haila et al. 1979), would naturally be that colonizations and extinctions within the archipelago are not correlated with population dynamics elsewhere.

We wish to examine a methodological point here, contrasting mapping censuses with one-visit studies. As species-abundance distributions tend to be depicted by using the logarithms of population size, even considerable errors in estimating population size do not greatly distort the distribution. This conclusion can, of course, be tested; and several experiments comparing mapping with one-visit censuses have shown quite similar species-abundance distributions (e.g., Järvinen et al. 1978a, 1978b; see also Table 1).

Species-abundance distributions can lead to a number of relevant insights. For example, the positive relation between the number of species and island area may be due to three different causes: habitat diversity, area, and sampling (i.e., if there are more individuals, there should be more species). It is difficult to test these al-
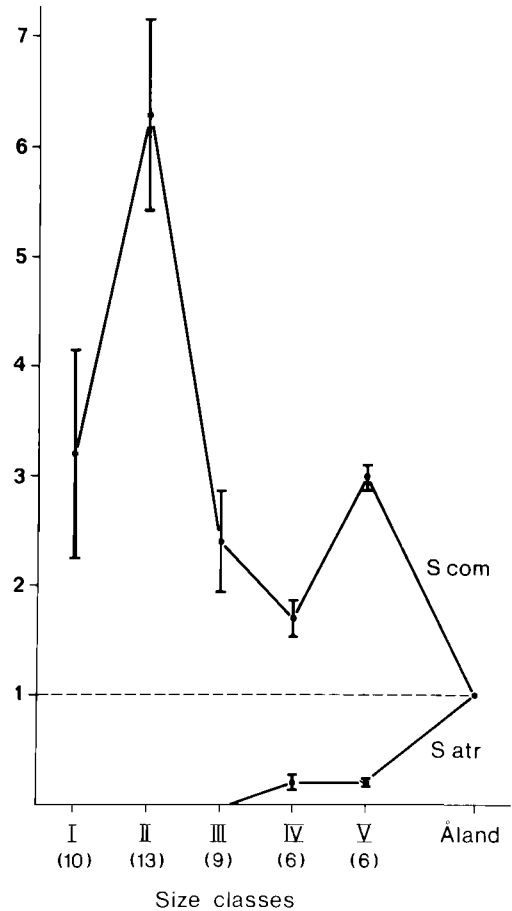


FIGURE 2. Prevalence functions for the Whitethroat, *Sylvia communis* (S com), and the Blackcap, *S. atricapilla* (S atr), in the Åland archipelago in 1976–79. Island classes were defined on the basis of the numbers of species (the group boundaries are 1–5, 6–10, 11–20, 21–30, and 31–60 spp.). Prevalence estimates, calculated for the pooled data of all islands in the same class, are shown with approximate estimates of SD (see Järvinen 1976). For details, see text.

ternatives critically (e.g., Connor and McCoy 1979), but the species-abundance distributions observed in censuses immediately suggest one test. Distribution-free rarefaction (Simberloff 1979; James and Rathbun MS; Engstrom and James, In press; Engstrom 1981) can be used to study species richness in samples standardized to an equal size. This makes it possible to test the null hypothesis that all differences in the numbers of species on different islands are merely a result of differing numbers of individuals, i.e., the sampling effect.
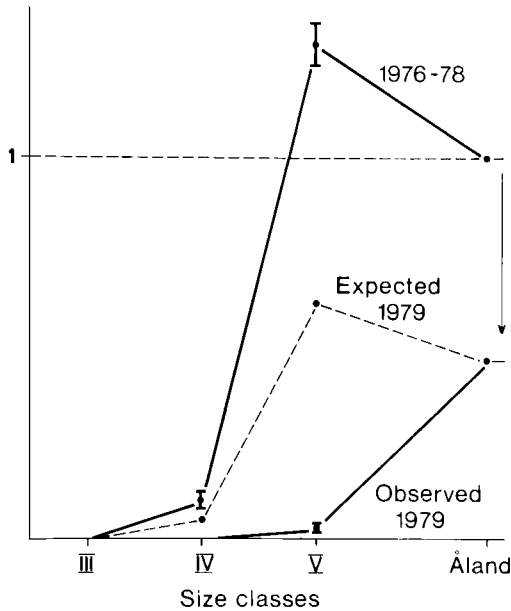
FIGURE 3. The prevalence function for the Field-fare (*Turdus pilaris*) in the Åland archipelago in 1976–78 and 1979 (expected and observed). The arrow on the right shows the population decrease observed on the mainland of Åland. See text for explanation.

## COLONIZING STRATEGIES: PREVALENCE FUNCTIONS

In his study of colonizing strategies of land birds, Diamond (1975a) constructed "incidence functions" on the basis of presence-absence data. An incidence function gives the frequency at which a certain species occurs on islands of different size classes in a certain archipelago. Incidence functions are necessarily fairly inaccurate because it is often impossible to study a sufficient number of islands in order to reduce the variance of the frequency estimates.

Census data can yield more information: while presence-absence data give only one record per island, quantitative censuses are able to indicate differences in population density among islands, and the number of records involved in such comparisons may often be great. The following new method, which we call the *prevalence function*, can be applied to analyzing census data. Prevalence functions are based on the average densities of a species on islands of different size classes. The average densities are compared with densities on the mainland (or an obvious species pool). If prevalence is 1, the species is equally abundant on the islands and on the mainland, and deviations from unity can be statistically tested.

In our study area the mainland of Åland is the obvious species pool. Comparing the average densities of a species on islands of different sizes with the density on Åland gives us an indication whether the species favors or avoids small islands—or, more accurately, whether it is comparatively numerous or scarce on small islands. Figure 2 gives an example comparing two European warblers, the Whitethroat (*Sylvia communis*) and the Blackcap (*S. atricapilla*). It is obvious that the former has comparably high densities on small and intermediate islands, while the latter is never found on the smallest islands and only rarely on the larger ones.

It is apparent that prevalence functions allow us to define different colonizing strategies; there may be species favouring small islands comprising patchy habitats, and there may also be species requiring large islands with continuous extensive tracts of habitat. The main point, however, is a deeper one.

An obvious hypothesis generally neglected in insular ecology is that the distribution pattern of a species in an archipelago is mainly determined by the availability of suitable habitat (Abbott 1980). It is feasible to refine prevalence functions if quantitative census data are available from different habitats (Y. Haila, O. Järvinen and S. Kuusela, in prep.). Our approach has been as follows. Nine broadly defined habitats were censused on the mainland of Åland (Haila et al. 1980a). As similar habitats characterize the archipelago studied by us in 1976–80, we can calculate the expected densities on the basis of the coverage of different habitats. In other words, prevalence functions can be so adjusted that gross habitat differences between the islands and the source area are eliminated.

For example, the two warblers in Figure 2 have an average density of 6.3 pairs/km² on the mainland of Åland (Haila et al. 1979). The high prevalence of Whitethroat on the islands is naturally interpreted as a consequence of the habitat composition of the islands (mosaic-like scrub is typical). Using the census data from different habitats on Åland, we would expect that the largest island studied separately by us, Ulversö, would support 25 pairs of Blackcap on the basis of the habitat composition of Ulversö. This is not the case, for we have observed one (1976, 1980) or two pairs (1979) there. Of course, the possibility of subtle habitat effects remains, because the match between insular and mainland habitats cannot be perfect and because our quantitative understanding of the autecological details of habitat selection is meager. In fact, the main reason eliminating Blackcap from most of the island forests seems to be a subtle habitat effect: the species favors tall luxuriant forests

on the mainland of Åland, but the average height of the trees is less (10–12 m) on the islands than on the mainland (16–18 m) in parallel habitats. Our preliminary results indicate that in many cases an apparent specialization to small islands is merely a result of the wide coverage of a favored habitat on small islands, and vice versa.

Another example based on prevalence functions shows patterns in annual variability. We have censused certain transects in our source area in several years, and we have thus been able to follow annual fluctuations in populations. A marked decrease occurred in the numbers of the Fieldfare (*Turdus pilaris*) after the severe winter of 1978/79. Assuming that the decrease was proportional on the islands studied, we calculated an expected prevalence function for 1979 on the basis of our data from 1976–78. However, the losses suffered on the islands were (Fig. 3) disproportionately heavy, and the "colonizing strategy" of the species looks quite different before and after the population crash. We raise one possible hypothesis here, but do not pursue the point further: the observations are compatible with the hypothesis that in our study area islands are suboptimal for the Fieldfare compared with the source area, so that densities in our islands are a function of abundance on the mainland.

## CONCLUSION

We conclude by stressing our take-home message. The theory of island biogeography has certainly led to an outburst of insular studies. In order to understand insular ecology, however, it is not necessary to restrict attention to qualitative presence-absence data. On the contrary, using quantitative census data can lead to many novel insights and ways to look at insular communities. The quantitative census methods should be chosen according to the actual needs of the biological problem studied, and here one-visit censuses, with a possibility to cover a much larger number of islands per unit effort, may often be superior to more accurate but time-consuming methods.