Conservation biology in agricultural habitat islands

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During the last 50 yr the Scandinavian landscape has been considerably altered because of changes from traditional agricultural practices to modern and efficient techniques. This change has resulted in large areas of monocultures (e.g., cereals, oil seed) but also abandonment of areas which earlier were used for grazing or hay production. Following this development, common problems for a sustainable biological diversity of agricultural land are habitat disappearance, decrease in habitat quality, influences on dispersal and interspecific interactions and increased importance of stochastic events. The five case studies presented in this paper focus on the effects of modern agriculture on animal and plant populations: 1) Species richness and diversity of carabid beetles were highest along edges between agricultural fields and woodland, and on habitat islands; 2) Bird species number, in relation to abundance, was higher on small than large forest-like habitat islands, due to edge conditions or habitat variability on the small islands; 3) Predation on blackbird nests was higher on small woodland islands than on larger ones, and this was particularly related to young and subordinate breeding blackbirds being forced to choose smaller islands as nesting sites; 4) Traditional agricultural environments supported a richer pollinator fauna than isolated habitat islands in an efficiently utilized agricultural landscape, and as a result of poor pollination seed set was also lower in the latter environment; 5) Grazing is an important factor in the pollination of the rare herb *Senecio integrifolius*. Even though seed set was positively correlated with population size, grazing may be detrimental to seed production or favourable to seed germination. Generalizing, species in boreal agricultural land are either derived from steppe environments with present source areas within this farmland or from the boreal forests and then often with sink populations within the farmland.

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The agricultural landscape in Scandinavia is under the influence of human activities and has been so for the last 6000 yr (Berglund 1969). Therefore, animals and plants of the agricultural landscape are adapted to human disturbance, even to the extent that some species cannot survive without agricultural activities. For example, grazing by cattle or mowing with machines creates necessary conditions for plant and animal species. Traditional agriculture allowed a mixture of different habitats from undisturbed natural environments, and wooded pastures to cultivated fields and therefore also a high biological diversity. However, two extreme changes have become an increasing threat to plants and animals during the last century. First, the economy of modern agriculture force farmers to establish large fields that are easily managed. Ditches, habitat islands (stone piles or shallow soils covered with vegetation) and other irregularities in the fields are considered as obstacles and are therefore often removed. From a conservation point of view this development is often

detrimental, because populations are fragmented and migration is reduced. Secondly, the large-scale abandonment of farming due to surplus production of agricultural products in western Europe has resulted in re-forestation, often with monocultures of spruce. This change causes problems for species that need habitat disturbance, i.e. species adapted to grazing, or species that need open areas.

During the nineteenth century the amount of farmland increased markedly and was used more efficiently than earlier. The agricultural landscape was characterized by a small-scale mosaic of fields, meadows, and grazed forests. A special feature of the Swedish agricultural landscape is the relatively high proportion of woodland. The mosaic has changed considerably during the last century, in particular during the last 50 yr, since government grants, subsidies, and technological development have allowed greater specialization and efficiency. The area of cultivated land and the number of farms have decreased, while the size of fields has increased to follow the size of machinery (Table 1). There is less animal husbandry and many meadows and pastures have either been converted to arable fields, or, more commonly, been afforested with spruce. This period is also characterized by an increasing reliance on pesticides (Odsjö 1988) and artificial fertilizers (Table 1). Residual habitats (e.g., habitat islands, ditches, and ponds) have been removed, and field edges have been made as straight as possible to allow efficient farming. The prognosis is for an even more monotonous landscapes since there will be a concentration of agriculture to the most productive soil (Heurling 1988). The flora and fauna of the residual habitats have been impoverished by many of these changes, and edge effects from agricultural practice, especially drift of pesticides and fertilizers from adjacent fields, have further contributed to the change. Of the four hundred species on the Swedish Red List of threatened vascular plants, three hundred belong to the traditional agricultural landscape (Ingelög 1988), and the number of threatened species will almost certainly increase in the near future. Re-establishment of traditional land-use as a method to increase habitat quality is unrealistic, except in small reserves. Instead, conservationists must identify the crucial stages in the life cycles of key species and any

conservation management has to be adjusted to satisfy the demands of these species.

Modern agriculture has thus resulted in severe problems for wild animals and plants. The five points below summarize some of the more important problems: 1) *Habitat loss.* Efficient modern agriculture results in the loss of natural habitats essential for many animal and plant species, such as ponds (e.g., reproduction of frogs), ditches (e.g., nest sites for bumblebees), and wet and flooded meadows (foraging sites for birds). 2) *Habitat quality.* A decrease in the quality of habitats has reduced their suitability for certain animals and plants (e.g., change in grazing intensity or use of pesticides and fertilizers). 3) *Dispersal.* The number of habitat islands has decreased resulting in increased isolation and reduced dispersal between islands (Merriam 1984). 4) *Stochastic events.* Small and isolated populations may face reduced gene flow and hence decreased heterozygosity (e.g., Franklin 1980, Ledig 1986). When a population becomes small and/or isolated, it becomes vulnerable to extinction through genetic, demographic, and environmental factors that may interact (Soulé and Simberloff 1986). 5) *Interspecific interactions.* Interspecific relationships (e.g., predator-prey and pollinator-plant) are probably particularly sensitive to disturbance since effects on one trophic level can affect other levels (Janzen 1974, Gilbert 1980, Wilcove et al. 1986).

These points also suggest that agricultural habitats provide excellent research areas from a conservation biology point of view. This chapter includes five case studies, each addressing one or several of these questions. The case study on critical habitats for beetles and the study of bird diversity in the agricultural landscape both deal with organisms specializing in steppe habitats which may require specific conservation measures because of the high level of human influence and the extreme spatial and temporal instability of habitats. The effects of stressful conditions on the maintenance and dynamics of populations can profitably be studied in agricultural habitats. Important lessons for conservation biology may be obtained from studies of the distribution of species and individuals, differential reproductive success, and interspecific interactions under the stressful conditions of modern agriculture. The agricultural landscape can thus be considered a model system for the study of conservation biology in an increasingly stressful world with habitat deterioration, alterations in species composition and distribution, and climatic change. This approach is adopted in the case studies of interspecific interactions in agricultural habitat fragments. These studies include an analysis of predation on birds' nests and its effect on the distribution of individuals in relation to source-sink problems, an analysis of the effects of habitat fragmentation on pollination and seed set by plants, and the effects of habitat quality and grazing intensity on plant reproductive success and ultimately plant population size.

Table 1. Changes in Swedish agriculture during the 1900's. From Svensson and Wigren (1986).

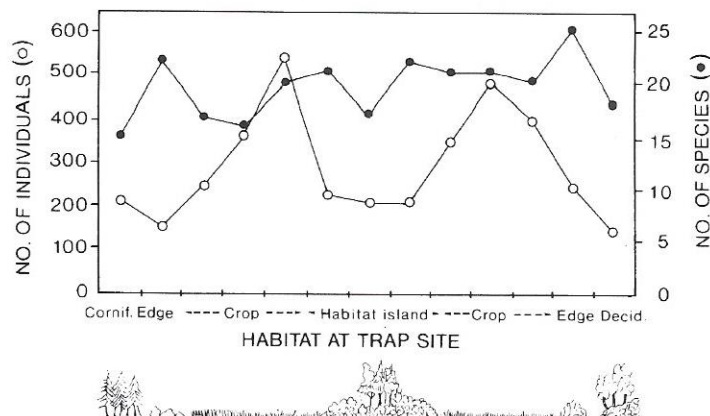| Factor	1917	1950	1980
Farmers, % of population	45	23	5
Area of arable land (1000 ha)	3 800	3 600	3 000
Area of meadows (1000 ha)	1 000	650	350
Number of farms (1000)	307	280	120
Number of dairy cows (1000)	1 800	1 700	650
Artificial fertilizers (kg N ha^{-1})	2	15	80
Pesticides (tonnes year^{-1})	0	3 000	8 000

Fig. 1. The numbers of individuals and species of carabid beetles caught in a transect line of pitfall traps set over different habitats at a study site in central Sweden in 1983. The habitat at each trap is represented schematically under the graph. The numbers of individuals or species caught in the pairs of traps differed significantly between the habitats.

Case studies

Critical habitats for carabid beetles on farmland

From a conservation stand-point the critical habitats are those with the highest diversity of species, or the habitats that are essential for continuing survival of particular species on farmland. In this study carabid beetles, which are sensitive indicators of habitat quality (Thiele 1977, Freitag 1979), were surveyed on farmlands around Sjö castle, west of Uppsala in central Sweden, to directly measure the relative numbers of species and their diversity in the different habitat components. This enabled us to evaluate the different components of Swedish farmland and ascertain which habitats were essential to maintain the diversity of species, and make predictions on the likely effects of changes in agricultural management.

Carabids were sampled with a 450 m transect line of 13 pitfall traps set over a variety of farmland habitats. There were thus two traps in woodland, two on edges adjoining the fields, six on the fields and three on a large (ca 1 ha) wooded habitat island in the middle of the field. The pitfall traps consisted of two 850 ml plastic containers buried flush with the ground and 70 cm apart. A piece of wood, 70 cm long and 10 cm high, was placed along the ground between the two containers forming a barrier that deflected the beetles into either container (Wallin 1985). There was substantial cannibalism among trapped beetles so a little detergent was added to a solution of 50% ethylene glycol in the bottom 4 cm of each container to kill and preserve the beetles. The traps were emptied weekly between mid-May and the first week in October 1983.

Pitfall trapping has been criticized as an inappropriate method for comparing the relative numbers of carabids in different habitats (Greenslade 1964, Duffey et al. 1974, Thiele 1977). The catches in pitfall traps depend not only on the densities of the different species but also on their activity patterns which are related to temperature and seasonal differences in behaviour (re-

viewed in Thiele 1977). This was not a problem in this study because the traps were established in the different habitats for most of the season and there was little difference in temperature among the trapping sites. Apparent differences in abundances of carabids in different habitats may be more a reflection of differences in the structure and density of vegetation rather than actual differences in the densities of carabids, because dense vegetation impedes their movements and reduces the probability of capture (Greenslade 1964, Thiele 1977). In this study, this problem was alleviated by clearing the vegetation for ca 50 cm around the traps. Clearing around traps makes them more efficient and reduces the differences in catchability between habitats that differ in vegetation structure and density (Greenslade 1964).

Despite the problems, pitfall trapping is the only effective way of sampling a whole community of carabids over the whole season in a variety of habitats. Direct methods, such as quadrat sampling, are impractical in habitats like woodlands with low densities of carabids (Greenslade 1964, Thiele 1977). Furthermore, direct methods can produce misleading data on the relative abundances of species in a community because they are a single snapshot of the community structure and the maximum numbers of species peak at different times of the season (Thiele 1977, Wallin 1985). Two indications support the reliability of the pitfall trapping in this study. First, most individuals were caught in arable fields followed by edges and fewest were caught in woodland which follows the pattern found by quadrat sampling and mark recapture estimates of densities. Second, Greenslade (1964) suggested that comparisons between different habitats are valid if the highest abundances are obtained from the densest, and more obstructed, habitat. We found the greatest abundances in the crop fields and edges which had similar dense vegetation and the lowest abundances in the sparsely vegetated woodlands and habitat islands.

Plotting the number of species and the number of individuals caught in the habitats in the transect gives

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an immediate impression of their distribution (Fig. 1), but there is no simple relationship between the number of species and the numbers of individuals. The highest number of individuals were found in arable fields where there were few dominant species. The highest number of species seem to be associated with bushy edges between fields and forest, but there were relatively few individuals at these high diversity edges. Fewer species were found in monocultures of arable field or woodland, and the lowest number of individuals were found in the forest inhabited by a few shade tolerant species. This distribution gives an impression of the relative carabid fauna in the different habitats, but does not help us separate which habitats are critical in maintaining a high diversity of carabid beetles.

Measurements of diversity are strongly affected by sample size, because with higher sampling effort there is a higher likelihood of collecting more species (Williams 1964, Magurran 1988). The sampling effort is uneven in the transect shown in Fig. 1 as most traps are in the crop fields. This problem can be overcome by rarefaction techniques that estimate the expected number of species in each sample if all the samples were of equal size (Hurlbert 1971). However, all information on the relative numbers of the different species is lost in rarefaction and we are simply left with the number of species expected in each habitat (Williamson 1973). To overcome this problem of unequal sampling we have used the data from two traps in each habitat, thus both traps in woodland, both traps on edges, two of the six traps on the fields, and two of the three traps on the habitat island. There was no significant difference in the number of individuals or species caught in the pairs of traps within each habitat, but there were significant differences between the habitats (Fig. 1).

A total of 2026 individuals of 49 species were caught in the eight traps (for species list, see Jennersten et al. 1992). The species were ranked in decreasing total abundance and showed the typical log normal pattern (Fisher et al. 1943) of a few abundant species, some fairly abundant species and many relatively rare species. Three measures of species diversity were calculated. First, the number of species or species richness is the simplest index but gives no indication of their relative abundance. Second, the inverse Berger-Parker index (May 1975) gives a measure of the dominance of the most common species for each habitat, so that a low value indicates that the most common species is the major constituent of the sample and hence there is probably a low diversity. Finally, diversity was measured with the log series which is a robust parametric diversity index which is very useful in discriminating differences among habitats (May 1975, Taylor et al. 1976, Magurran 1988). From such calculations it was clear that most species were found in edge habitats which also had a low dominance and a high diversity. The number of species was similar in fields, woods and

on the habitat island, but the lowest diversity was in the fields. Although there was one more species on the habitat island than in the woods its diversity was lower because of the greater dominance on the habitat island.

There were marked differences in the distribution of species among the four habitats. When comparing the usual habitat preferences of the different species as described by Lindroth (1986) and Thiele (1977), it was clear that most individuals were found in their expected habitats. There were several eurytopic or widespread species, such as *Pterostichus melanarius* and *P. niger*, that were caught in all four habitats, but specialists such as *Amara brunnea* and *Calathus micropterus* only occurred in the woods or on the wooded habitat island, or at the edge such as *C. melanocephalus*, *A. lunicollis* and *A. communis*. The fewest species were found in the fields and many were eurytopic species although some species were confined to fields, such as *Trechus quadristriatus* and *Bembidion quadrimaculatum*, while *A. apricaria* was a commensal species favoured by farming. Although the habitat island was dominated by *P. melanarius* and *Carabus hortensis* it had a rich beetle fauna including many of woodland species and some rarities such as *Cychrus caraboides* and *Licinus depressus*, both of which prey on land snails.

To summarize these relationships of species and their relative abundances in the different habitats the data have been analyzed with canonical correspondence analysis (CCA), a powerful multivariate ordination technique that readily identifies the habitat components that are important in determining the distribution of the species and the habitats contributing to species diversity (ter Braak 1986, 1987). CCA combines regression and ordination into a direct multivariate gradient analysis that substantially improves the power to detect unimodal relationships between species and external variables, which cannot be detected with the usual parametric techniques such as principal components analysis. CCA reduces the complex multivariate data to two axes or eigenvectors that optimally shows the maximum differences between the distribution of the species in relation to the weighted averages of the environmental factors and shows where the main species diversity is (Jongman et al. 1987). The statistical significance of the optimal distribution can also be tested with Monte Carlo simulations and the output can be plotted for visual interpretation. The relative association of each species with particular habitats is shown by their distance from the weighted average of each habitat.

Figure 2 shows the ordination diagram of the species scores, the habitat scores and the centroids of the diversity indices. The first two axes were significant (explaining 67% of the variance) and showed that the species were associated with different habitats and that there was a simple gradient from those species in crop fields, through those on edges and habitat islands to
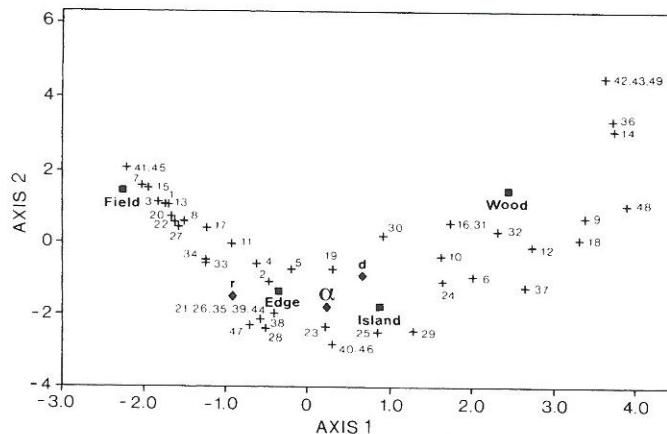
Fig. 2. Ordination diagram based on canonical correspondence analysis of the carabid beetles caught, for details see text, and the habitats around the pitfall traps (see Fig. 1).

those in woodland. Those species near the weighted average of the different habitats are associated with those habitats, thus the woodland species are on the right of the figure, the field species on the left and the edge and island species in between. The field species are distinct from the woodland species and those on the habitat island, and although there is overlap of the species on edges and habitat islands each has distinctive species. To test whether the observed differences could be attributed to chance, we ran Monte Carlo simulations with the first eigenvalue as a statistic test and 99 random data sets all yielded a lower eigenvalue showing there are significant differences in species among the four habitats. Note that the weighted averages for the diversity indices (richness r, dominance d and α) are placed near the edge and island habitats. This confirms that these habitats are the most diverse and suggests that their removal will disproportionally reduce the overall diversity of beetles on farmland. However, the carabids on these small habitat islands and narrow edges are probably vulnerable to the effects of agricultural practice on the fields, especially aerial drift of sprayed pesticides and fertilizers.

Bird diversity in the agricultural landscape – the importance of small habitat islands

Several previous studies have emphasized that a large area is important if a sample, e.g., a reserve or habitat island, is to include a full set of species (e.g., Opdam et al. 1984, Nilsson 1986). An obvious explanation is that a large island will contain a larger sample of individuals or habitats, making it more likely that more species are represented. However, this cannot be considered a real biogeographical effect. The result is also valid for situations where only islands in the upper size range are large enough to satisfy the area requirements of some species. This is an important consideration when discussing area effects, but it must not lead to too far-reaching general-

izations. In some situations, the importance of some species' area requirements are offset by other mechanisms, even creating an opposing pattern.

This case study addresses the general question: is there a relation between habitat island size and species diversity? The study was conducted in an extreme agricultural habitat. Most islands were small (Fig. 3), with only few typical forest bird species represented. The islands included constituted a typical sample of those found in the area with a variety of habitats like deciduous woodlands, aggregations of bushes and abandoned fields. Two aspects of island size were treated. First, is there a correlation between the size of a given habitat island and the number of species when all aspects of vegetation and isolation of an island are controlled for? It is also important to remove the effect of species numbers that merely arises from an increased number of individuals on larger islands (Hurlbert 1971).

The second aspect is whether one large habitat island has more species than several small islands of the same total area. This much debated question, commonly referred to as SLOSS (single large or several small; Simberloff and Abele 1982), has been analyzed by grouping the investigated habitat islands (see below) into four groups of successively smaller islands but of the same total area.

Territory mapping (Anon. 1970) was used to determine the number of breeding pairs on 238 habitat islands in the agricultural landscape of Scania, southernmost Sweden. The relative number of species was used as a measure of diversity and was calculated by dividing the actual number of species on a habitat island by the expected number of species obtained from the rarefaction analysis.

The relative number of species was negatively correlated with habitat island size after correcting for isolation, shape and vegetation (partial correlation analysis) (Fig. 3A). Thus, small habitat islands had relatively more species than large islands. Intraspecific competition may preclude two pairs of the same species coexist-

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Fig. 3. A. The relationship between the size of habitat island and relative number of bird species of 280 habitat islands in Scania, southern Sweden. The line is the linear regression line. B. The number of bird species per habitat island size group. The islands are grouped into four size classes (1 = largest islands, 4 = smallest islands) where each group has a similar total area.
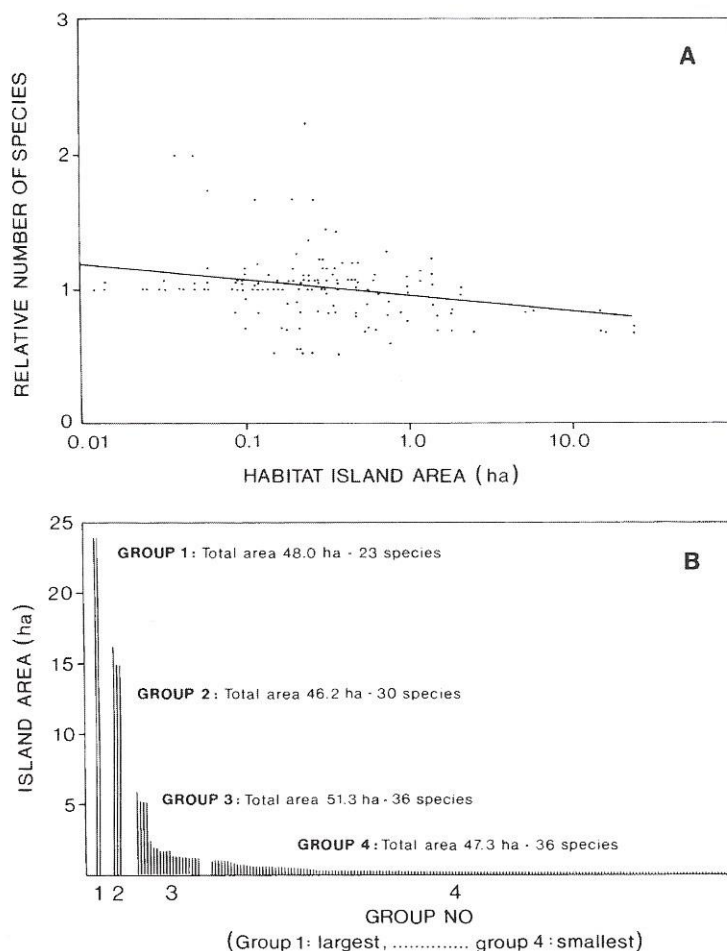
ing on a small habitat island, but allow two pairs of different species to coexist.

Aggregating the habitat islands into four groups revealed that the small islands collectively accommodated more species than larger islands of the same total area (Fig. 3B). Two mechanisms may explain this pattern: 1) Edge species like yellowhammers *Emberiza citrinella* may be more abundant on a aggregation of small islands than on a single large island because they have relatively more surrounding fields and/or forest periphery. 2) The small islands may collectively have a higher variation of habitats and thus be able to accommodate more species than a single large habitat island.

The present study does not explain the mechanisms behind the observed pattern. However, from a conservational point of view, if local species diversity is a concern, it points to the relative merits of small habitat islands. We do not say that large islands should be sacrificed in favour of small ones. However, mere size is not a reason for discriminating against small habitat islands.

Bird nest predation and habitat island size

Studies of biogeography in habitat islands often make the assumption that all individuals of a given species are similar. The simplest distribution of similar individuals of a particular species is the ideal free distribution (Fretwell 1972). According to this distribution, individuals occur in relation to the size of habitat islands provided island size exceeds a minimum requirement. This will, however, only be the case if everything else is equal. This is usually not the case because biological and stochastic processes vary in relation to habitat island size and because individuals differ in competitive ability (Fretwell 1972). A number of different processes may affect the distribution and the abundance of species on habitat islands, including intraspecific and interspecific interactions and stochastic processes.

Nest predation is a major cause of reproductive failure in birds and may be affected by the size of habitat islands in a number of ways. First, small habitat islands have a relatively larger circumference than larger islands, and since predation often is an edge-
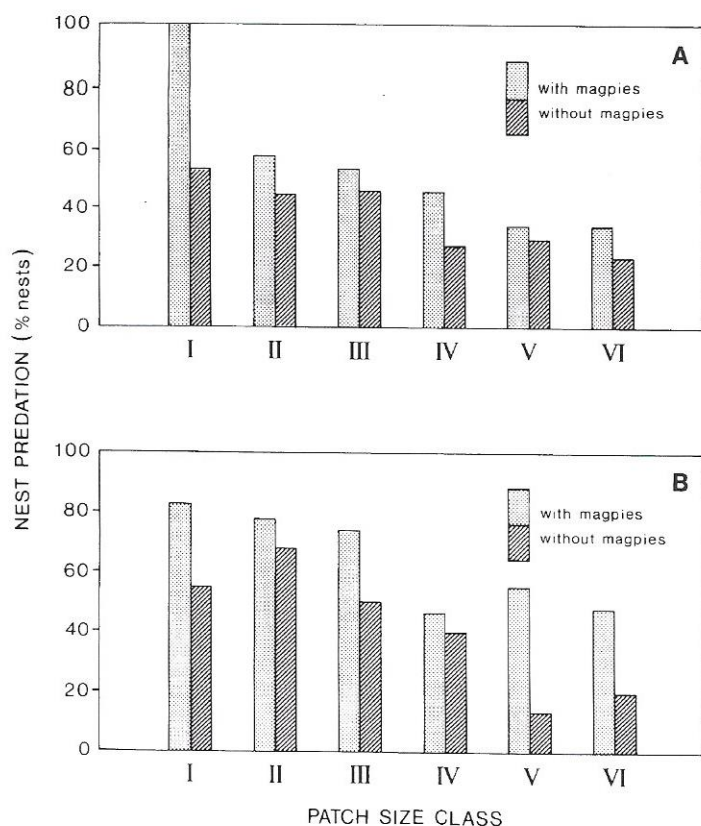
Fig. 4. A. Predation rates on natural blackbird nests (% nests preyed upon) in relation to habitat island size in the Kraghede study area during 1971–1974 and 1977–1982. Sample sizes are 5–37 nests. B. Predation rates on blackbird nest with plasticine eggs (% nests preyed upon) in relation to habitat island size during 1987. Sample size is 18 nests per group. Patches either had (left bars) or did not have breeding magpies (right bars). Patch size classes are I = 0.05–0.1 ha, II = 0.1–0.2 ha, III = 0.2–0.4 ha, IV = 0.4–0.8 ha, V = 0.8–1.6 ha, VI = 1.6–3.6 ha.

effect (e.g., Gates and Gysel 1978, Andrén 1995), individuals breeding on small islands will suffer from increased predation. Second, individuals nesting on small islands may differ in quality from those nesting on larger ones. For example, risks of nest predation may be related to individual differences in the ability to build well-concealed nests that are relatively safe from predation. Third, smaller habitat islands may contain fewer and less suitable nest sites than larger ones. This study describes variation in the intensity of nest predation on blackbird *Turdus merula* nests in habitat islands of different size, and islands of different size may therefore differ in attractiveness. Data on the age distribution and the reproductive success of blackbirds suggest that competitively superior individuals prefer large habitat islands to small ones (Møller 1991).

The frequency of nest predation by magpies *Pica pica*, on blackbird nests was monitored in habitat islands covered with elm *Ulmus glabra* L. at Kraghede, northern Jutland, a typical Danish farmland habitat (Møller 1988). These species are suitable because they are common breeding birds, and breeding magpies are either present or absent on particular islands. The intensity of predation on blackbird nests was significantly negatively related to habitat island area, and the presence of a single pair of magpies increased the risk of nest predation (Fig. 4A).

Differential nest predation in relation to habitat island size could be caused by differences in the quality and thus the behaviour of individual blackbirds. By placing plasticine eggs mimicking blackbird eggs in old nests of blackbirds it was clearly demonstrated that the risk of nest predation still decreased with increasing habitat island area. Blackbirds on islands harbouring magpies more often suffered from nest predation than did blackbirds on other islands (Fig. 4B).

Differential nest predation in relation to habitat island area could also be due to differences in the availability of safe nest sites. This appeared not to be the case since blackbird nests on small islands, where nest predation was especially common, were more effectively hidden in safe sites like buildings, coniferous trees and hedges (Møller 1988). The risk of nest predation on small islands was therefore high despite the more effective concealment of nests. In conclusion, differential predation on blackbird nests in relation to the size of habitat islands appeared to be caused by area per se and not by other confounding variables.

As individuals are expected to maximize their lifetime reproductive success, blackbirds should compete for access to sites that are relatively free from predation. Thus blackbirds are not predicted to follow an ideal free distribution relative to the size of habitat islands, but rather an ideal despotic distribution in

Fig. 5. A. Frequency of breeding blackbirds (% patches with blackbirds) in relation to habitat island size during 1979–1982. B. Population density of breeding blackbirds (pairs ha^{-1}) in relation to habitat island size during 1979–1982. C. Age distribution (% yearlings) of breeding blackbirds in relation to habitat island size during 1971–1974 and 1977–1982. Blackbirds were caught in mist nets. For patch size classes see Fig. 4.
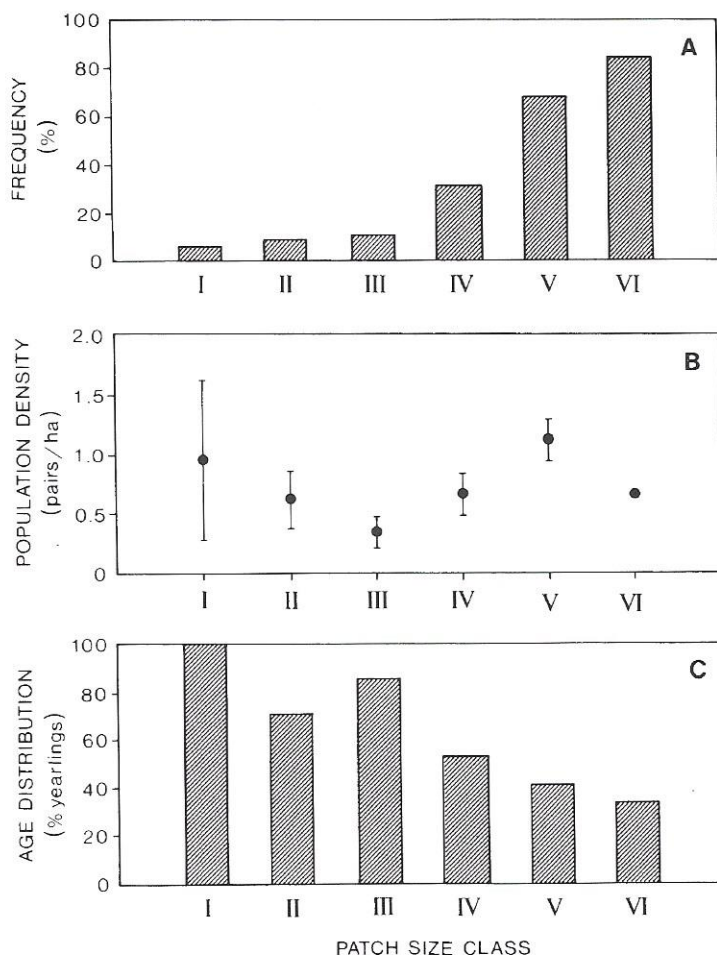
which competitively superior individuals occupy the superior habitats (Fretwell 1972). Is there any evidence for such a despotic distribution?

Habitat islands differed in their attractiveness. Blackbirds occurred on smaller islands less frequently than on large islands (Fig. 5A), but the population density of blackbirds on differently sized habitat islands showed no consistent pattern with habitat island area (Fig. 5B). The relatively high population density of blackbirds on small islands may be due to less intraspecific and interspecific competition for food (Møller 1987).

The age distribution of blackbirds in relation to habitat island size provided evidence for an ideal despotic distribution, since young blackbirds are competitively inferior (Bruun 1969). The fraction of yearling blackbirds caught in mist nets during the reproductive season decreased from 100% in the smallest islands to <40% in the largest ones (Fig. 5C).

Reproductive success of blackbirds measured as clutch size was not significantly related to habitat island size (Fig. 6A). Mean clutch size was predicted to increase with increasing habitat island size, because older blackbirds, on average, lay larger clutches (Snow 1958), and the blackbirds on large habitat islands were older. However, clutch size did not vary with island size (mean clutch size range: 4.4–4.6 eggs), but brood size increased from 2.5 fledglings per nest in the smallest islands to >4 in the largest ones (Fig. 6B). Differential reproductive success in relation to habitat island size was mainly caused by a lower nest predation risk in larger habitat islands.

The reproductive success of blackbirds differed among habitat islands since success increased with area. This was mainly due to high nest predation rates on small habitat islands. Interspecific interactions such as predation differed among habitat islands and affected the distribution of individuals and this markedly influenced the contribution of different habitat islands to overall reproductive success of the population. Small habitat islands were sinks while large islands were sources.
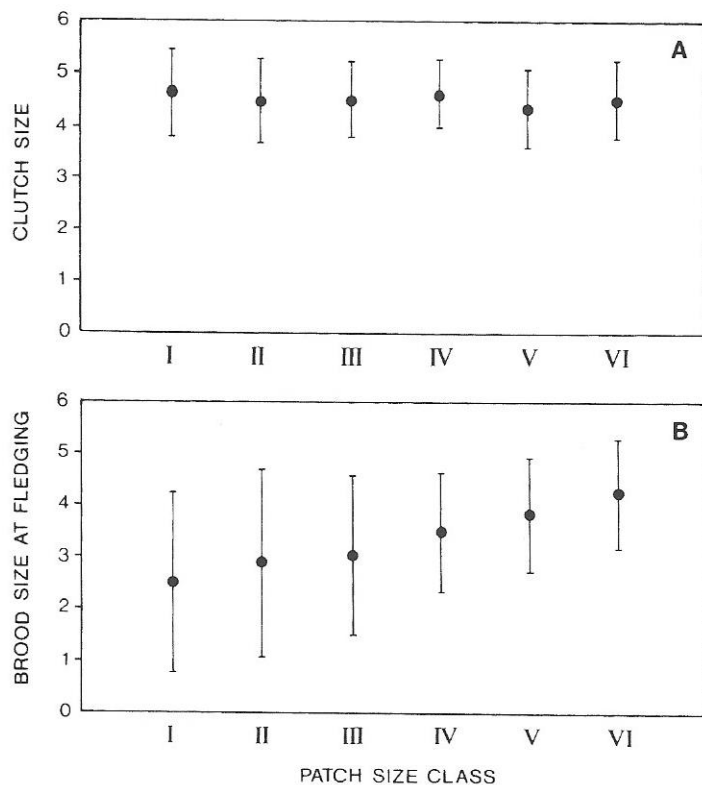
Fig. 6. A. Clutch size of blackbirds in relation to habitat island size during 1971–1974 and 1977–1982. Sample sizes are 8–37 clutches. B. Brood size of blackbirds at fledging in relation to habitat island size during 1971–1974 and 1977–1982. Sample sizes are 4–37 clutches. Values are mean ± SD. For patch size classes see Fig. 4.

Pollination ecology on habitat islands

Geometry of plant populations, e.g., size, density, and shape, influences pollinator behaviour and thus pollen flow (Handel 1983). Therefore, fragmentation of habitats may affect both pollinating insects and the plants relying on pollinator services. Here we compare the abundance and diversity of flower-visiting Lepidoptera and Hymenoptera and the seed set of perennial plants on habitat fragments in a modern agricultural area (island area) and in a traditional agriculture area consisting of a mosaic of different habitats (mainland area). We ask three questions: 1) Are there differences in the abundance and diversity of flower-visiting insects between the island and the mainland areas? 2) Are there differences in seed set between differently sized plant patches? 3) Is there a difference in seed set between the two areas?

The study was conducted at two sites in the province of Dalsland, south-western Sweden. The island site is a agricultural district consisting of eight habitat islands of 0.1–0.5 ha. Each island is surrounded by arable fields, mainly barley or oats. The mainland site is situated ca 50 km north of the island site and consists of four meadows in a mosaic of forests, abandoned and cultivated fields, thus representing the traditional agricultural landscape. The entire study area can be regarded as a transect from modern to traditional agricultural land.

Insect and plant diversity were measured in transects on eight habitat islands at the island site and in four fields of the mainland site. Insect visits to specific plants were observed in 1×2 m squares for 15 min periods. Seed set was analyzed by marking individual plants prior to flowering (for details, see Jennersten 1988).

The island and the mainland sites were quite different in species composition. A proportional similarity analysis (Wolda 1981) showed that the occurrence of flowering plants and flower-visiting insects were grouped within areas (Fig. 7). The transects within the two areas were more similar in species composition than between the areas, though this is less clear-cut for plants than for insects. The encounter rate of insects per unit area and unit time differed significantly between the two areas. In July 1986 6.5 times as many flower-visiting insects were found at the mainland site as at the island site. A nested ANOVA showed significant differences not only between sites, but also between transects within sites. Spatial variation was higher at the island site than at the mainland site.

Data from both 1985 and 1988 demonstrated a significant temporal variation within the island site. In 1988, temporal variation in insect abundance was neither significantly correlated with flower abundance nor with number of flowering species of plants, but with the occurrence of bountiful plant species. For example, when *Sedum telephium* began to flower, bumblebees and in particular honeybees appeared in large numbers

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on the islands. The number of visiting insects was positively correlated with the abundance of *S. telephium* flowers on islands and accounted for 42.3% of all flower visits (N = 710). Other "popular" plants were *Linaria vulgaris* (14.8%), and *Hypericum maculatum* and *H. perforatum* (12.0%), which when common attracted numerous bumblebees.

Possible explanations for the differences between the two sites are 1) effects of isolation: the islands are separated by large areas of arable land with low availability of food source plants for insects (except irregular occurrences of crops like clover and rape) as well as nest sites for bumblebees. 2) Environmental effects: the islands are not cultivated because soils are too shallow or are bedrock outcrops, and they are thus sensitive to periods of drought. For example, at the end of June 1988 following two months of very dry weather almost no plants flowered.

A patch of a plant species can be regarded as a model for a fragmented and an isolated population. Geometrical features of an island affect seed set of a plant species (e.g., Handel 1983), and, for example, in the sticky catchfly *Viscaria vulgaris* (Caryophyllaceae) individuals in large patches produce more seeds than individuals in small patches (Jennersten and Nilsson 1993) (Fig. 8). Curiously, the visitation rate per flower of the main pollinator, long-tongued bumblebees (e.g., *Bombus hortorum*), is independent of patch size, so individual

Fig. 7. Proportional similarity (Sörensen-Renkonen-Czekanowski's index, Wolda 1981) on 8 habitat island at the island site and 4 meadows at the mainland site. Top graph describes flower-visiting insects (Lepidoptera and Hymenoptera) and bottom graph the flowering plants found in transects.

flowers in small patches have a similar probability of a visit compared with flowers in large patches. One hypothesis to explain this phenomenon might be the foraging behaviour of bumblebees. Individual bumblebees are known to concentrate their foraging to one food source plant (their "major" food source, sensu Heinrich 1976, 1979). They also visit a number of other plants' flowers, but to a lesser extent (their "minor" food sources). This behaviour might help bumblebees keep track of changes in their environment. It is possible that *V. vulgaris* acts as a "major" food source when growing in large patches and as a "minor" when in small patches. Other studies have found positive correlations between patch size and number of flowers per foraging bout of bumblebees (Sie and Baltus 1987). The result from the plants' point of view may be a much more efficient transfer of conspecific pollen grains in large patches and a higher probability of heterospecific pollen transfer in small ones. Thus, there may be a higher deposition of *V. vulgaris* pollen on stigmas of flowers in large patches despite more visits per flower in small patches.

Intriguingly, other factors may prevent an increase in patch size. In *V. vulgaris* predispersal seed predation was also positively correlated with patch size; a higher proportion of seed capsules were attacked mainly by a geometrid moth (*Perizoma hydrata*) and a curculionid beetle (*Sibinia viscariae*) in large than in small patches (Jennersten and Nilsson 1993). Additionally, the presence of a sterilizing fungal disease (*Ustilago violacea*) was positively related to patch size (Jennersten 1985), possibly for the same reason as for high seed set; the more efficient foraging of bumblebees, which is the main disease vector.

The maiden pink *Dianthus deltoides*, a perennial, protandrous, caryophyllaceous herb of sunny habitats on sandy soils, grows commonly in the mainland site and in two of the island sites. Its flowers close at night – hence it can only be visited diurnally by dipteran flies and in particular by butterflies, its primary pollinators.

Dianthus deltoides flowers received fewer visits at the island site than in the mainland site due to the lower abundance of anthophilous insects (Jennersten 1988). The seed set also differed between sites, being higher at the mainland site in both 1986 and 1987, but not in 1988 when precipitation was unusually high during the flowering period. A hand pollination experiment in 1987 established pollen availability as the limiting factor since hand pollination increased seed set at the island site but not at all at the mainland site (Fig. 9). The seed set of hand-pollinated flowers was similar at the two sites. Resource limitation is not a probable explanation for these differences because the addition of water and fertilizer had no effect.

Bagged flowers also produced similar numbers of seeds at the two sites. In addition, the seed set of bagged flowers did not differ from the seed set of
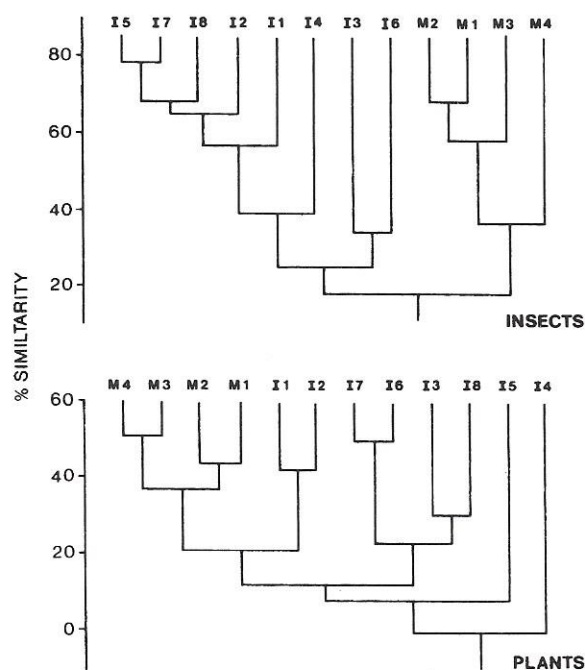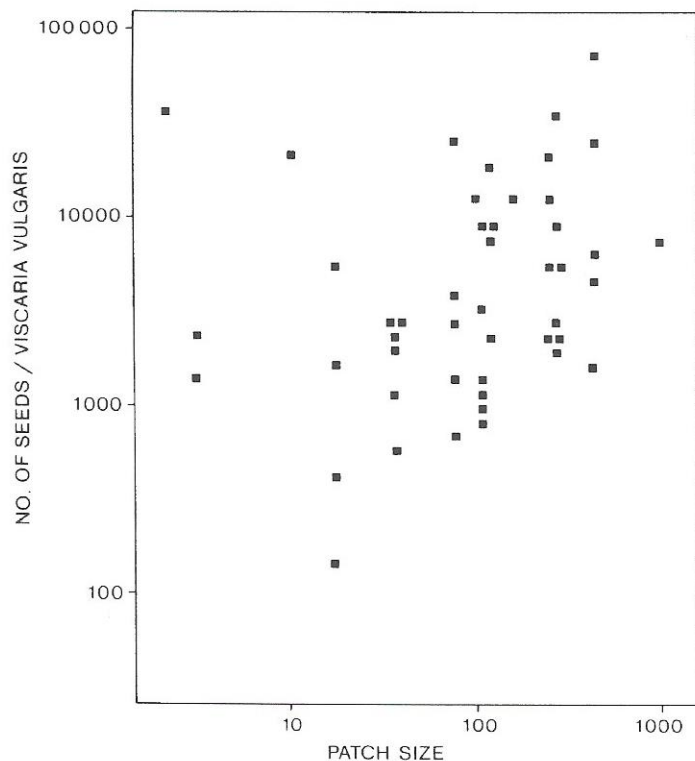
Fig. 8. Number of seeds per *Viscaria vulgaris* plant in relation to plant patch size (= number of plants/patch) in Dalsland, southwestern Sweden 1982. Note the log-log scale. From Jennersten (1985).

naturally pollinated flowers at the island site, indicating that a large proportion of the seeds produced at the island site is self-fertilized. The flowers are clearly self-compatible and self-fertilized seeds germinate. The island site has probably been under influence of agriculture for at least one hundred years and it is therefore likely that the two islands have been isolated for a similarly long time. One may therefore speculate over the genetic status of the island plants. Self pollination leads to a lower heterozygosity and hence a higher probability of the expression of deleterious alleles that may interfere with reproductive capacity or make the plants more vulnerable to environmental stress.

A seed germination test revealed that seeds from the island populations have a more narrow amplitude in terms of germination time: most seeds from the island site germinated within 10 days (90.0%) while only 37.7% of the mainland seeds germinated within the same period, indicating that the island population may be genetically less heterogeneous than the mainland site. Seedlings from the two localities were thereafter planted in pots and placed in a greenhouse during Feb.–March 1989. The plants were measured once every week and after eight weeks they were transferred back to their places of origin. The plants were subsequently planted in four blocks, two at the mainland site and two at the island site. Every second plant in each block originated from the mainland population while the other came from the island site. Plants from both

populations were thus planted at both their site of origin and at the other site.

In the greenhouse seedlings from the two localities had similar survival but leaf development (number and length) was superior for plants that originated from the island population. In the field, place of origin had no effect on survival nor on plant performance (number of stalks, flowers and height (except second year)) but the plants performed differently among the four blocks, probably due to difference in soil quality (Fig. 10). Thus, visible effects of origin on plant survival and performance were not detected in this field experiment, suggesting that this fragmented population does not suffer because of low heterozygosity.

Reproductive success of the field fleawort in relation to habitat fragmentation and habitat quality

This study estimates fitness parameters in relation to habitat fragmentation (patch size) and habitat use (grazing) of natural populations of a threatened plant, the field fleawort *Senecio integrifolius* (Asteraceae). Three questions have been asked: 1) Does seed set differ among populations of different sizes? 2) Do quality differences among habitats due to grazing intensity lead to differences in reproductive success among populations? 3) What is the relative contribution of

Fig. 9. Seed set (% ovules that developed into seeds) in *Dianthus deltoides* following different experimental treatments: flowers were bagged to prevent insect visits (Bag), flowers were artificially hand-pollinated (Hand), hand-pollinated and given water (Water), hand-pollinated and given artificial fertilizer (Fertilizer), and not manipulated to provide a natural control (Control) at the mainland site (grey) and the island site (hatched bars). Vertical bars denote standard error of mean (modified from Jennersten 1988).
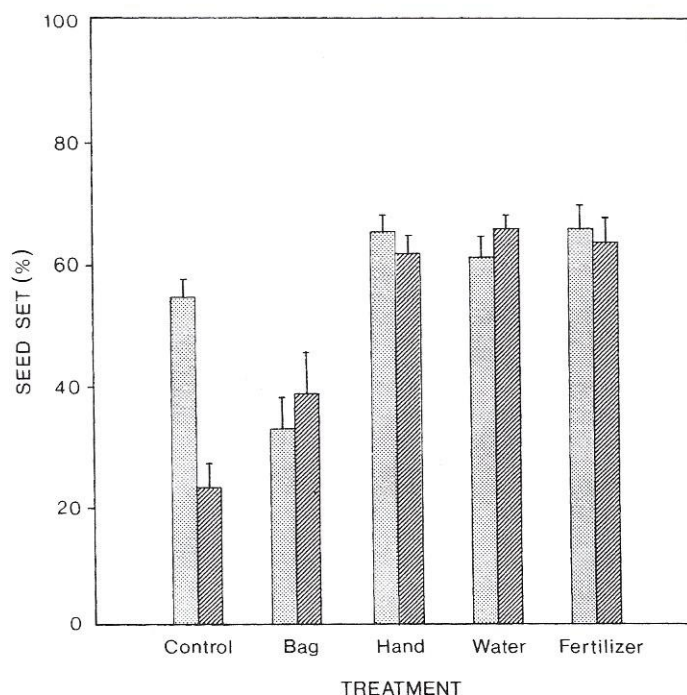
population size and habitat quality to reproductive success?

Senecio integrifolius is a perennial herb of grazed pastures usually producing one leaf-rosette bearing a single stem. Individual plants flower iteroparously with an interval of several years. Flowering frequency and generation time differ among populations depending on grazing intensity; plants at intensively grazed sites flower more frequently and become older than plants at ungrazed sites (Widén 1987). The plant is self-incompatible (Widén 1991) and visited by a variety of insects, mainly dipteran flies (Widén 1986). Germination is light-dependent and recruitment occurs mainly during the first autumn. The species lacks a soil seed bank. (For details of the dynamics of natural populations, see Widén 1986, 1987, 1988, 1993).

The study was carried out in six of the eight known Swedish populations of *S. integrifolius*. The populations vary in size and structure from < 10 flowering stems in one or several small patches of a few square metres each, to over 8 000 flowering stems in one continuous population of ca 1 ha (Widén 1988). The species had a wider distribution in Scania, the southernmost province of Sweden, during the last century (Nilsson and Gustafsson 1977). Any migration among populations is unlikely, mainly because they are distributed on well-separated habitat islands in the modern agricultural landscape with few interjacent sites of sufficient quality. The main reason for the retreat of the species is the use of artificial fertilizers and lack of grazing by cattle (Widén 1987). The extant populations are all situated in habitats that are not artificially fertilized due to their

topography, and at sites that are still grazed or were grazed by cattle until recently. In the following we will define the quality of the habitats of the natural populations in terms of the grazing practice.

Seed set was measured in natural populations 1980–1982. Seed set was positively correlated with population size (Fig. 11A). This is probably an effect of density dependent seed set, an hypothesis that was experimentally tested in cultivation. Plants derived from seeds sampled in the largest natural population (Tosteberga) were planted in four patches in a semi-natural habitat in the Fredriksdal Botanical Garden, Helsingborg. Twenty-five plants were evenly distributed in each of 1, 4, 25 and 100 m². From Fig. 11B it is evident that there is a density effect on seed set in the experimental population. Hand pollination in one natural population and in cultivation revealed that pollen limitation explains most of the variation in seed set (Widén 1991, 1993).

Individual plants were mapped in permanent plots 1980–1982 in four populations with different levels of grazing intensity. The number of stems produced as well as the number of successful stems (not grazed before seed dispersal) were recorded. The probability of a stem being grazed before seed dispersal varied from 0.1 at the site with the lowest grazing intensity to 0.95 at the site most intensively grazed (Table 2). Thus, very few plants dispersed their seeds at the most heavily grazed site (Widén 1987). Based on the number of successful stems and the average number of seeds per head, seed production in permanent plots was estimated for 1980-1982. Although the number of stems differed
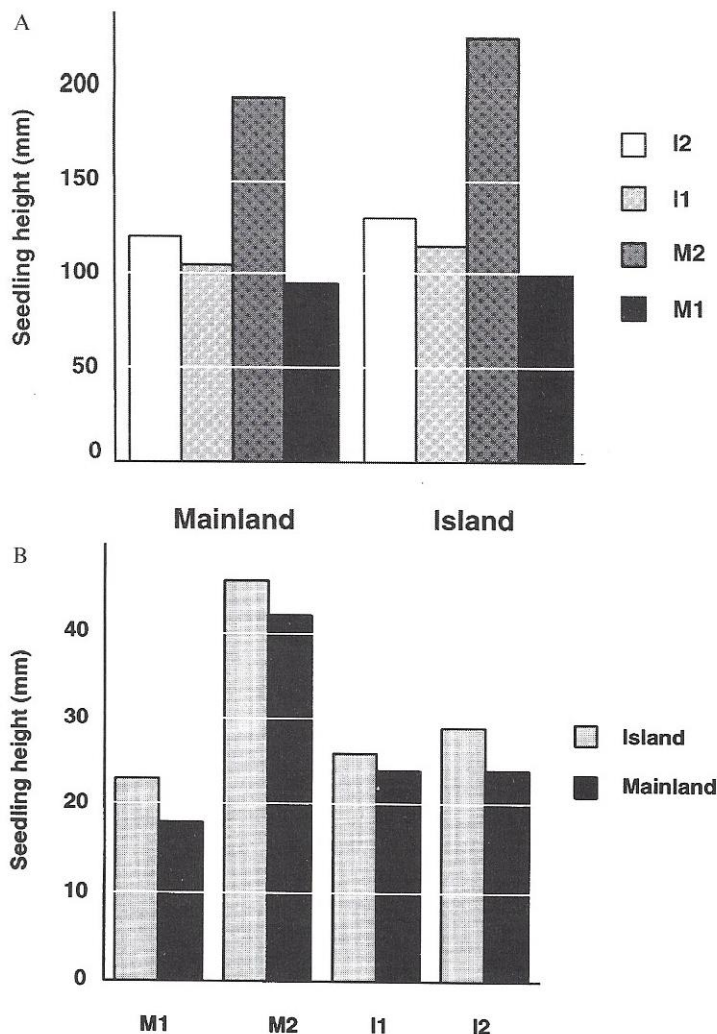
A

Mainland   **Island**

B

Fig. 10. Plant performance in *Dianthus deltoides* originating from two populations. A. Seedling development during 9 weeks in the greenhouse. B. Seedling preformance (height) during the second year in the field. Plants originating from the mainland and island populations were planted on two locations at the mainland site (M1, M2) and two locations at the island site (I1, I2). Origin did only effect height the second year but location did all four year.

four-fold among populations, the number of seeds produced in permanent plots differed with a factor of 220 (Widén 1987, 1988).

The number of seedlings recorded from July 1980 to October 1982 in the permanent plots varied 25 times among populations. These seedlings represent from 1% germination of the produced seeds at the lightly grazed site to 75% germination at the heavily grazed site (Table 2). Thus, intensive grazing has a detrimental effect on one life cycle stage (seed production), but a very favourable effect on another (seed germination).

In populations with < 100 flowering stems seed set is less than half of that in large populations (Fig. 11). However, the influence on reproductive success from population size is much less than the influence from habitat quality, e.g., grazing intensity (Table 2).

Grazing is an essential component of a high-quality habitat for *S. integrifolius*. Intensive grazing favours seed germination (Table 2) and survival of seedlings

and older plants (Widén 1987). The sites of two of the eight populations of *S. integrifolius* were not or only lightly grazed for many years (Widén 1987), and these populations are now probably extinct. However, intensive grazing can decrease the number of successful stems to a small fraction of the potential of the population and thus decrease the population growth rate. Four of the extant populations have been over-grazed during the last decade, much reducing the potential population size (unpubl.). It would be easy to improve the quality of the habitat also under intensive grazing management by changing the timing of grazing. Grazing usually starts in early May and seed dispersal of *S. integrifolius* is usually over in late June. If grazing starts at the time of seed dispersal most stems would be successful, and this would rapidly increase population size. Thus, the quality of the habitat could be improved markedly by changing the grazing practice.

Fig. 11. Seed set in *Senecio integrifolius*. A. Average seed set and population size in six natural populations, 1980–1982. Each population is represented by one dot each year (for two populations only 1980–1981). B. Seed set (mean ± SE) in cultivated plants derived from Tosteberga. Twenty-five plants at each plot were planted at four densities.
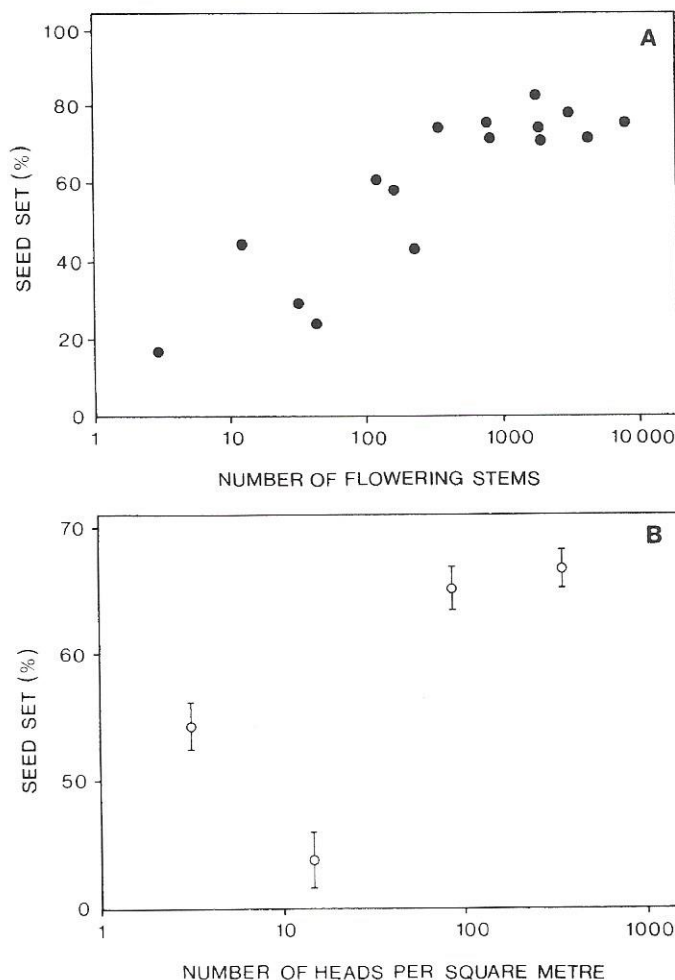
General conclusions

An important aim of nature conservation is the preservation of a diverse fauna and flora. One way of achieving this is to preserve large areas of pristine habitats, but such reserves are usually in remote areas and relatively inaccessible. Most peoples' experience of nature is of residual habitats in managed environments such as the agricultural landscape, which although not pristine are worth preserving. Most of the fauna and flora of farmland survives on these suboptimal remnants, but the main stronghold of the species that originated in natural open habitats (e.g., steppe species) is on farmland. Nature conservation can be seen from different perspectives with two extremes, the global and the local perspective. From a global point of view, the preservation of all species is a worthy task. From a local perspective, it is important to maintain a high species diversity. It is essential to stress these differences because different goals may call for an emphasis on different conservational measures. The present paper takes the local perspective, and we ask: How do we preserve species diversity and a mosaic of remnant habitats in farmland?

The species-rich traditional habitats of farmland are being converted to arable fields or coniferous plantations that support few species, and modern management removes many of the small islands of scrub and other remnant habitats that might form refuges for some species. A mixture of habitat islands, meadows, scrub and deciduous woodland is necessary to maintain a high species diversity. The increasing dominance of large featureless arable fields and coniferous plantations will seriously impoverish the fauna and flora of much of south and central Sweden, and the only remaining diversity will be in nature reserves where traditional habitats are protected. The quality of remnant habitats in farmland can, however, be improved by paying attention to crucial life stages of indicator species when planning the management. Grazing has been one of the most important factors for the present distribution of many plants and animals adapted to the traditional agricultural landscape. Even in the near future, grazing in habitats where no artificial fertilizers are used will be

Table 2. The probability of reproductive success at different life cycle stages in four natural populations of *Senecio integrifolius* (1980–1982). Individual plants were recorded in five permanent plots (1 m^2) at each site every second week during the vegetation season. The sites are arranged from low to high intensity of grazing (left to right). The estimates are based on data from Widén (1987).

Life cycle stage	Kverrestad	Grödby	Tosteberga	Benestad
Seed set	0.79	0.75	0.74	0.42
Successful seed dispersal	0.90	0.74	0.38	0.05
Germination	0.01	0.08	0.11	0.75

essential for preserving species-rich pastures. This, however, requires more knowledge of the life cycle of sensitive species than presently available.

A problem facing conservationists is whether to preserve a single large or several small reserves (SLOSS). A large reserve supports larger populations that are genetically and demographically more stable than populations on a small reserve. However, the single large population is vulnerable to a catastrophy such as disease, which would be less likely to affect all parts of a subdivided population on several small reserves. In the context of an agricultural landscape relatively more species may occur on small habitat islands (e.g., Fig. 3B). However, it is important to identify the population sources and sinks before effectively determining whether to preserve a number of small islands or a single large one of the same area.

The distribution of individuals and species across habitat islands may be affected by size-related differences in habitat quality, and also by intraspecific and interspecific interactions occurring at different frequencies across a gradient of fragments. What are the implications of interspecific interactions for nature conservation? The intensity of intraspecific and interspecific interactions is likely to vary with the size of habitat islands, in the same way as predation on blackbird nests and the resultant intraspecific competition for territories, pollination of *Dianthus deltoides*, and the effects of grazing on *Senecio integrifolius*. Such differences in the suitability of islands may lead to an ideal despotic distribution because differently sized islands differ in profitability. This will have consequenses of the relative contribution of different sized islands to recruitment at a local scale.

The reproductive success of blackbirds differed markedly among habitat islands of different size. Smaller islands are likely to be population sinks with a negative population growth, and they are only maintained by a steady flow of individuals from more productive islands, i.e. sources. This probably also applies to other species. Sources and sinks can only be identified if essential demographic parameters such as natality and mortality are known (Pulliam 1988). The true sources may be far outside small study areas and hence cannot easily be identified. The major lesson for nature conservation is that vast areas of suboptimal habitat, even those having high population densities, cannot be assumed to be

sources (van Horne 1983, Pulliam 1988). Intensively managed agricultural areas, because they have few habitats and are structually homogeneous, are likely to be sinks for most species. However, they might also be source areas for a few species that are pre-adapted to this type of environment, for example steppe species.

Habitat islands are characterized by a low abundance of flower-visiting insects, but with large spatial and temporal variation. This variation is to a large extent governed by the abundance of highly rewarding nectar/pollen plants that attracted insects from afar (e.g. honeybees). Thus, availability of flowering plants on habitat islands is important for a rich pollinator guild. Too few pollinators can result in a reduced seed set, increased self-fertilization and, eventually, a lower degree of heterozygosity and perhaps extinction. However, in plants reduced heterozygosity is not as serious as in animals since plants can deal with for example environmental heterogeneity through phenotypic plasticity. Isolated, animal-pollinated plants can adapt by changing breeding system. For example, *Dianthus deltoides* may be able to change from protandry to homogamy and thus a higher degree of self pollination.

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