Dispersal and population turnover: the founding hypothesis

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During the German Occupation of the Netherlands (1940-'45) I became an active member of the NJN (Dutch Youth Association for the Study of Nature) and became especially fascinated by insects. At first, my interests mainly concentrated upon bumblebees and other wild Aculeates. After the German Occupation (1945) I started to study Biology at Leiden University where I soon discovered the biogeographical works of Lindroth on Fennoscandian Carabid beetles, the first part of which had just appeared (1945). My interests in Carabid beetles was especially evoked by the possible role of wingdimorfism among these beetles, which phenomenon was creatively used by Lindroth to reconstruct the history of the colonization of Fennoscandia by carabids after the last Glacial Period (Lindroth, 1949). In 1948 the srudents of Biology that started in 1945 had to participate in a course at ITBON (Institute for Applied Biological Research in Nature), where I met Joop van der Drift, who worked on the decomposition of litter. He sampled arthropods in the litter with the help of pitfalls, and used for that the biscuit tins left behind by the Canadian soldiers, who liberated the Netherlands from the German Occupation in 1945. He showed me that especially Carabid beetles could be sampled quantitatively with this kind of pitfalls. Therefore, with my NJN-workgroup on insects I tried out this technique, also with the still available Canadian biscuit tins (25x25 cm, 30 cm deep), and found it highly successful. After my Master's examination (1951) I became the assistent of Donald Kuenen, the first Professor of Ecology in the Netherlands. He ordered me to find out what would be the best methods and techniques to take up again the Meijendel-research, i.e. investigations in the dunes near The Hague to disentangle the so-called "Web of Life". I adviced to let make 100 pitfalls, and to sample with these the surface fauna in different dune habitats, especially Carabid beetles. In this way we would be able to follow the faunistic changes that would occur after the inundation of certain dune valleys as it was planned by the Dune-Waterworks of the Hague: see den Boer (1956a,b; 1958a,b). When in 1958 I moved to Drenthe to do research at the Biological Station Wijster of the Agricultural University in Wageningen, I decided to test my ideas on population dynamics, dispersal and population turnover, which I developed in Leiden during my investigations in the Meijendel-research, with Carabid beetles as test objects. Therefore, I let

construct pitfalls at the TFDL (Technical-Physical Service for Agriculture) in Wageningen, and placed pitfalls in all kinds of natural or semi-natural areas around Wijster (in the centre of the province of Drenthe in the Netherlands). By sampling carabid populations of many species and in many different kinds of habitat during as many years as possible in the first place I hoped to test the popular **regulation-hypothesis** against my ideas about **stabilization of numbers** by different kinds of stochastical processes (o.a. den Boer, 1968; Reddingius & den Boer, 1970). The history of this aspect of my research is described in *"The development of a concept"*. All carabids caught in the pitfalls were ckecked on the development of wings (e.g. den Boer, 1962), in order to test my ideas on the significance of dispersal in population turnover.

From the very start of my investigations in Drenthe I realized that the relationship between dispersal and population turnover (founding/extinction) might be of principal importance for the development of a well-founded Nature Conservation. In connection with the following, at this place I must emphasize that my choice of working with carabids does in no means restrict my conclusions as far as advices for Nature Conservation are concerned, as is often claimed by opponents of my work as being not applicable to e.g. Vertebrates. Caribids have nothing special as compared with other groups of animals, such as butterflies, moths, birds, lizards, mice, or other animals loved by naturalists. My choice for carabids is simply based on some apparent advantages as objects of study: (1) they are easily and releably sampled quantitatively with the help of pitfalls; (2) all species having populations in a selected habitat are sampled with the same set of pitfalls; (3) in almost all species the powers of dispersal depend on the development and utility of wings, only in a few species with big adults dispersal by walking may be significant; (4) for comparative studies there is a favourable relation between numbers of unwinged, wingdi(poly)morphic and constantly fully winged species respectively; (5) the larvae of most species are generalized predators of soil-arthropods, whereas the adults are predators or scavangers of surface arthropods, by which the binding to habitats mainly depends on physical factors (weather/climate and soil/vegetation properties); (6) the taxonomy of the species is well-studied, though not for all species the larvae are already described adequately: (7) the adults are easily manipulated in experiments, individually marked, bred in the laboratory or raised in encloseres in the field, etc.

As reliable and comparable sampling of carabids might improve the significance of carabids as objects of ecological studies, in 1964 a group of ecologists in the Netherlands decided to execute a sampling experiment with rhe same setup of pitfalls in the same kind of habitat (light deciduous wood) in different parts of the Netherlands, in order to be able to standardize

both sampling and comparing of results. One of the sampling sites was a young poplar-alder wood planted in 1958 in the just reclaimed and drainaged Zuiderzee-polder East-Flevoland (section N60). Carabids that would have founded populations there could only have reached that site, which was surrounded by agricultural fields, by flying in from the mainland, so that for me the results of that sampling experiment might be a nice example of the founding of populations in a pristine area. Therefore, I hypothesized that wingdi(poly)morphic carabid species would have settled down there as winged (macropterous) individuals, and that the shortwinged (brachypterous) morph –if present in the samples- could only have been brought in there by macropterous females that were already inseminated by a brachypterous male before flying in from the mainland. Hence, the percentage macropterous adults of di(poly)morphic carabid species in the catches was expected to be much higher than in old populations of the same species on the mainland, e.g. in Drenthe This hypothesis was convincingly confirmed for all wingdimorhic species found in the samples from that site (den Boer, 1970, 1971a; Haeck, 1971). As data and theories about colonization -especially by carabids- of islands and coastal areas draw much interest (e.g. Palmén, 1944; Lindroth, 1949, 1963), we decided to organize a symposium on dispersal and dispersal power (the possibilities to cover distances and to found populations) of carabid beetles, where we could place our results from the new polders more in perspective. This symposium took place in 1969 in the new building of the Biological Station Wijster, where we also invited some specialists from abroad, e.g. Carl Lindroth, Ernst Palmén, Hans-Ulrich Thiele. One of the 'mechanisms' by which populations were thought to be 'regulated' is intraspecific competition when density becomes very high, by which a certain number of individuals would be forced to leave, i.e. when the 'carrying capacity' of the habitat would be surpassed dispersal as a kind of 'overflow' from too high densities would bring density within more tolerable values again. As I could not find any relation between yearcatches (being releable relative estmates of densities) and dispersal among the carabid species studied at this symposium I proposed to replace this **'overflow'** **hypothesis** of dispersal by the **'founding'** **hypothesis,** i.e. individuals dispersing from a population would increase the chance of founding new populations (den Boer, 1971a). Not only the founding of new populations in East-Flevoland (above) illustrated the dispersal power of full-winged carabids, but also the catches of such individuals in window traps (den Boer, 1971a; van Huizen, 1977, 1979). Nevertheless, Lindroth thought it to be difficult to accept that individual carabids would leave the population irrespective of living conditions becoming adverse, but he agreed that my data did not give any support to the 'overflow' hypothesis of dispersal. On the other hand, when such dispersing individuals

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would arrive in an adequate site to found a new population (Haeck, 1971) the genes favouring such behaviour would be multiplied again, so that natural selection, though generally working against dispersal behaviour in longer existing populations, will be favouring it again in newly founded populations for at least some time. After this symposium in Wijster in 1969 new arguments were found to support the 'founding hypothesis': (1) also inseminated females leave populations and are caught in window traps (van Huizen, 1977,1979); (2) Cees den Bieman found that amiong specimens of the forest carabid *Calathus rotundicollis (=piceus)* leaving the wood are significantly more full-winged specimens with functional wingmuscles than among those that stay behind (den Boer et al., 1980). By estimating 'relative wingsizes' (surface of wings related to surface of elytra) most wingdimorphic species –and also many monomorphic macropterous species- appeared in fact to be polymorphic, i.e. showing a broad range of relative wingsizes, with mainly those with the greatest wings being active flyers and being caught in window traps (den Boer et al., 1980). (3) Later some of my coworkers discovered that in some species the production of dispersers is restricted to relatively favourable conditions concerning food and temperature, e.g in the monomorphic macropterous species *Nebria brevicollis* only then wingmuscles will develop (Nelemans, 1987b), and in the wingdimorphic species *Calathus melanocephalus* the genes for the development of functional wings and wingmuscles will only be expressed under such conditiond (Aukema, 1990), i.e. when the population is not in danger. Note, these processes favouring dispersal occur independently of density; they can even be stimulated in the laboratory in isolated specimens. (4) Also, in both species dispersing females produce more eggs than 'stayers' (Aukema, 1990; Nelemans, 1987a.b), i.e. also in this respect dispersers are especially equiped to found new populations, and thus nicely illustrate the **'founding hypothesis'**. Not only monomorphic macropterous and wingdi(poly)morphic species show dispersal out of populated habitats, also monomorphic brachypterous species do. For instance, big specimens of the functionally completely unwinged *Carabus problematicus* walk away from the woods around the village of Kralo and can be caught at 1 to 2 km's from these woods in the heath area. Females lay eggs in the heath, larvae develop normally there, but most puppae die, so that there are not founded surviving populations of this species in the heath area (den Boer, 1970, 1971a; Rijnsdorp, 1980). Again, also this phenomenon does not show any relationship with densities in the paternal populations, i.e. it is not 'overflow', but individual 'dispersal'. .

After the symposium of 1969 we concentrated upon the present funcioning of dispersal in the cultivated countryside Drenthe, where suitable habitats are fragmented and often small

and highly isolated. I was especially interested in finding a quantitative expression for the significance of dispersal in connection with 'turnover' of populations, i.e. with the processes of founding and extinction of (parts of) populations in a highly ftagmented landscape. After many discussions with Hans Reddingius such an expression was found in DPS (Distribution of Population Sizes), being the relationship between the sum of the logarithms of the yearcathes –as estimates of yearly densities- of the species in our samples and the logarithm of the sum of all these yearcatches –as an expression of the quantitative presence of the spesies in our samples. The idea behind this formulation of DPS was: if a species is living in temporary (only for a short period suitable for reproduction) habitats, it will mainly be represented by low yearcatches in our samplings, whereas a species living in permanent (old and rather stable) habitats will mainly be represented by relatively high yearcatches in our samplings. The first kind of species will only survive in our area by showing a high level of dispersal in order to compensate for the high number of extinctions by frequent (re)foundings (high turnover). The latter kind of species will mainly survive in remnants of the original kind of natural habitat where it will have.lost much of its dispersal power, and as long as these habitat fragments are not very small in size and low in number these species will be able to survive for many years with a low level of turnover. DPS indeed expressed what I wanted to know, and the cumulation lines of the logarithms of the yearcatches plotted at probability paper nicely showed what are the effects of differences in dispersal power for carabid species in a cultivated countryside with fragmented habitats:

A-species (living in stable habitats) showed broken cumulation lines (few yearcatches with small numbers, more yearcatches with relatively high numbers) and the majority of DPS-values between 0.64 and 0.70;

B-species (living in temporary habitats) showed straight cumulation lines (yearcatches about normally distributed) and the majority of DPS-values between 0.76 and 0.81.

In 1975 I had prepared a manuscript about dispersal, DPS and population turnover. As I wanted to publish it in Oecologia I presented it to C.T. de Wit in Wageningen, the editor of Oecologia in the Netherlands. Cees de Wit thought the content of my paper very important, but much too long to be published in Oecologia. Therefore, he asked his coworker Rudy Rabbinge to study my MS and to find out how it could be reduced significantly, in order to be taken up in Oecologia. Rudy Rabbinge thought the MS too important to reduce it drastically. Therefore, Cees de Wit proposed to publish it in the Miscellaneous Papers of the Agricultural University Wageningen, and to add all original data.. He advised me to ask many copies, so that I could distribute it at a large scale. I ordered 500 copies of Miscellaneous Papers 14.

"Dispersal power and survival. Carabids in a cultivated countryside" (1977). As a member of the WRR (Scientific Council of Government policy) Cees de Wit thought my findings important in connection with the growing realization among policymakers that it becomes necessary to design a plan for management of nature and landscape. I don't know how far my conclusions played a part in the final design of the plan for Nature Management that was distributed more than ten years later (some policymakers used carabids to illustrate the consequences of habitat fragmentation, e.g. Winsemius). At least Rudy Rabbinge, who succeeded Cees de Wit in the WRR and Claus Stortenbeker, who added our group at the Biological Station Wijster to his department of Nature Management in Wageningen, were convinced of the importance of our work with carabids for Nature Management. I don't know how Paul Opdam, who at RIN (Government Institute for Research in Nature) had to underpin the Government Plan for Nature Management, got the idea to ask me who would be able to investigate the function of roadside verges as connection between semi-natural areas with the help of carabids (Vermeulen, 1993, 1994). By one of the discussions with Cees de Wit about measures to be taken to counterbalance habitat fragmentation he asked me to take over his editor job for Oecologia. So I was the Dutch editor of Oecologia from 1977 until and including 1998.

Hence, around 1980 I had reasons to suppose that my **'founding hypothesis'** (den Boer, 1977, 1979b; Thiele, 1977: Ch. 8) was known among policymakers as a useful guide for taking meaningful measures to remove or at least reduce the isolation between habitat fragments, and that the easy to sample and identify carabid beetles would be considered to be adequate test organims to evaluate the results. Therefore, I was surprised to learn that workers in Nature Conservation and Management almost exclusively refer to the 'Island Theory' of MacArthur & Wilson (1967) to underpin the measures that had to be taken to improve the isolation of habitat fragments. I was the more surprised, because the 'Island Theory' indeed is nothing more than a deductive theory, which is hardly based on sufficiently convincing facts about the effects of connection and/or fragmentation of islands. Moreover, our remnants of nature are not isles in the ocean, though for some organisms –but not for all groups-agricultural areas may be some kind of 'ocean'. In fact, the heart of the 'Island Theory' is rather trivial and simply based upon the regression-lines of Preston (1962): the farther away from the continent and the smaller the island the less organisms will have settled down there. Perhaps, exactly this simple and hardly to be doubted logic may apply naturalists, supported by the fact that the data of Diamond et al. (1976) could nicely be fitted with the regressions of Preston (1962). However, the 'Island theory' does not predict anything about the effects of

differences in dispersal power and population turnover of species. The population processes described by MacArthur & Wilson (1967) are the popular deterministic –and never proved convincingly in the field- theoretical constructions, such as 'regulation of numbers', 'competition between related species', 'habitat segregation between related species'..As far as relevant facts about special kinds of organisms are considered these are mainly birds. Because of that I was not impressed by the 'Island Theory' when I composed "Dispersal power and survival", and did hardly discussed this theory. To be able to make my objections against application of the Island Theory in Nature Conservation more widely known I gladly accepted the suggestion to contribute to a special volume of 'WLO-Mededelingen' on this kind of subjects (den Boer, 1983a). I constructed a computer-programme in which a group of species, with a range of dispersal powers as about found among my carabids, with in time stochastically differing sizes of reproduction and connected levels of turnover, living at a continent and dispersing randomly over an archipelago of islands with randomly different sizes and at randomly different distances from the continent. The species did not show any of the processes favoured in literature, such as 'regulation of numbers', 'competition', 'optimal fouraging', etc.; they just fluctuated in numbers, died out locally and were refounded, and dispersed over the archipelago according to their specific powers of dispersal. With this computer model I could exactly simulate all predictions made by the 'Island Theory'.and confirmed in literature by studies of numbers of bird species on islands. Hence, the 'Island Theory' is correct, because it is a trivial mathematical rule of thumb without any special biological meaning, In a next paper I gave a short summary of my 'founding hypothesis', illustrated with findings on carabid beetles (den Boer, 1983b), which were the basis of the model presented in the preceding paper (den Boer, 1983a). Apart from its trivial aspects illustrated by my model, there is a single interesting aspect in the 'Island Theory', the difference that is made between 'continental isles' (parts of a former continent that have become islands, e.g. because of a rising sea-level), and 'oceanic isles' (islands directly risen from the seabottom, e.g. by vulcanic activities or by growing corals). This difference also applies to natural areas on the continent: isolated fragments of former large natural areas are comparable to 'continental islands', and in the course of time such fragments will mainly lose species, especially those with low powers of dispersal. On the other hand, new natural areas, isolated or not (e.g. natural areas in new polders: Haeck, 1971) or planted wood, are comparable to 'oceanic islands', and in the course of time such new areas will have to build up their faunas by well dispersing species that settle down there (den Boer, 1970). But why refer to the 'Island Theory' if on the continent we want to make this difference when we can

also speak about 'fragments of old nature' versus 'new nature', made by human activities or by natural causes? Of course, we know that if we want to save species from old natural areas we will have to connect the remnants by newly made habitat that is thought to be suitable, and possibly may have to reintroduce the species already lost locally. In my opinion for workers in Nature Conservation on the continent the 'Island Theory' is of little use, other than a shortcut in conversations, bexause it does not give any understanding of the important and interesting variation in the phenomena we have to understand to manage Nature in such a way that biodiversity will be kept at an acceptable level.

Does all this mean that I reject the use of deductive rules or models? On the contrary, these can be of great help in directing our thoughts and giving us a general idea of what is common in a broad class of phenomena and processes. Possibly the best example of the usefulness of a deductive concept is the working out of the concept of 'Natural selection' by Charles Darwin. However, in this time of great hurry there is hardly any time to work out an idea or a concept, because everyone must be afraid that his idea is picked up by a colleague and is published rapidly under his name. As a consequence, many good ideas are published too early and often unseasoned. I had this problem too with my concept of **"spreading of risk"**; I had to publish it before I could work out convincing examples of its favourable effects (den Boer, 1968), and had to confine myself for the time being with simulation models to illustrate the logics of the idea (Reddingius & den Boer, 1970). Note, 'to illustrate' and *not* 'to prove'. Therefore, when in 1978 I again met Charles Birch and he remarked "You have more to propagate your 'spreading of risk' " I answered "I prefer to prove it" And I did so; for more information see *"The development of a concept"*. The drawback of early publishing a new idea or concept is, if it fills a need, that hardly anyons will take the trouble to start investigations to prove or disprove it; on the contrary, the interpretation of certain facts, which do not evidently match with the new idea or concept, or even distinctly point into another direction, is often 'adapted' in such a way that these facts do no longer contradict the theory. If such an 'adaptation' goes on for a long time it is hardly possible to convince your colleagues from the need to start anew; you are seen as a spoilsport. I had this experience when I tried to oppose to the 'regulation hypohesis'. Because of its deterministic formulation the 'regulation hypothesis' does not take account of the effects of genetic differences between individuals, and of the heterogeneity and changeability of the habitat (see further *"The development of a concept"*, and den Boer & Reddingius, 1996). This situation is not restricted to the 'regulation hypothesis', but is common to most popular ideas in population dynamics. It does also occur in discussions about competition between related species and exclusion (den Boer, 1980,

1983c, 1985a, 1986). This tendency to keep nature simple and to formulate natural processes, if possible, deterministically even slipped into Darwin's carefully prepared concept of 'Natural selection' as being 'Survival of the fittest' (den Boer, 1999). When also ecologists learned to work with computers it was too inviting to construct deterministic computermodels about natural processes and thus to keep all kinds of stochastical variation -whether being only unimportant noise or essential information- far away (den Boer & Reddingius, 1996).

How was the 'founding hypothesis' received? It was not received at all, in spite of the fact that Hans-Ulrich Thiele, who visited our symposium in 1969 and participated in the discussions with Carl Lindroth (den Boer, 1971a), supported my ideas adaquately in chapter 8 of his book (Thiele, 1977), and Andrewartha & Birch (1984) were enthousiastic and supplemented my findings with own data in chapter 8 of their new book. However, the book of Thiele (1977) only dealt with carabid beetles and will not have been read by other ecologists (at that time ecologists considered studying carabids as being waste of time). The new book of Andrewartha & Birch (1984) was considered by critics to be 'more of the same' –meaning more of the matter already discussed in their book of 1954- which will not have stimulated to study it closely. This superficial meaning of critics was a pity, not only because Andrewartha & Birch (1984) showed that both my 'spreading of risk' and my 'founding hypothesis' are general principles and not restricted to carabid beetles, but also distinctly discussed the different uses of the concept 'population', including my 'interaction group', which in many cases is the same as their 'local population', and in other cases synonymous with 'subpopulation'.

Because from my population-dynamical background I was already involved in estimating the parameters of the patterns of fluctuations of population numbers, I tried to develop methods to get an impression of the expected survival time of sampled subpopulations (den Boer, 1971b) –interactiongroups, den Boer, 1977- of carabid species with different powers of dispersal. As one of the most important parameters of population fluctuaions is the net reproduction value, i.e. the relationship between the density in year t and that the year before $(R= n_t / n_{t-1})$, I studied the frequency-distributions of R-values in different species, which are sufficiently accurately estimated by the yearcatches in two succeeding years (Baars, 1979a,b; den Boer, 1979a). Moreover, the distribution of R-values of the same species from different interaction groups (also from different sites) did not differ significantly; so that from each species a specific distribution of R-values could be obtained. With sufficient R-values such a distribution looked like a lognormal one. Hans Reddingius agreed and gave me the formula to calculate the fitting lognormal distribution (Appendix to den Boer, 1985a). With χ^2 it

appeared that none of the field-distributions of R-values differed significantly from its fitted counterpart. For each of 64 species we could simulate now realistic fluctuation-patterns of numbers by randomly drawing R-values from its fitted distribution. In the few cases where we had estimated actual density levels we could scale the simulations at the right density level and thus estimate expected survival values for the interaction groups concerned (random-range models). However, for most species at most sites estimates of actual density levels were not available, and although in some cases reasonable guesses of actual density levels seemed to work rather well, I tried to find another method to estimate expected survival times for which knowledge of actual densities is less critical. Such a method was found by evaluating the 'zero yearcatches': in many catch-series of most species there are years in which not a single specimen of that species was caught at that site. I wondered, whether such a 'zero yearcatch' indicated that the species in that year had actually disappeared from that sample-site (actual turnover, i.e. local extinction), or that local density had become so low that not even a single specimen could be caught in the entire year (pseudo-turnover). In order to be able to distinguish between these two possibilities, from the fitted lognormal of R-values for that species I simulated 500 random-range series over the number of years we had continuously sampled that site (between 4 and 16 years) at an absolute density level that I supposed to be sufficiently high for that species in an optimal habitat, but in fact the exact density level did hardly play a role in the following Next, I took from these 500 density series catches at the catch (x3) level of the highest yearcatch as it actually occurred for that species at that site, and could determine now how many 'zero yearcatches' in these 500 simulated series of catches may have indicated 'pseudo-turnover', In this way for each species at each sample site I got an estimate of the percentage of years with 'pseudo-turnover' that might be expected. With this %pseudo-turnover, summed over all sites, the % of years with 'zero yearcatches' for that species could be corrected now for all sampling years, by which the number of years an average interaction group of that species might be expected to survive could be estimated (den Boer, 1985a, 1990b). These survival values were close to what I expected from other –but less reliable- experiences, and in the only case for which survival values were directly estimated from the field, i.e. in *Agonum ericeti*, the value from my simulations appeared to fit nicely (de Vries & den Boer, 1990). For 64 carabid species sampled in 89 sites over 23 years these values of % corrected turnover (and connected mean survival times) were indeed hihgly significantly correlated with the corresponding DPS-values (den Boer, 1990b: fig. 5). This not only means that DPS appears to be a reliable estimate of the relationship between dispersal and population turnover, but also that my

'founding hypothesis of dispersal' (den Boer, 1971a) need no longer be considered an hypothesis, at least not for carabid species. The supposed relationship between dispersal power and turnover of populations is a reality, the dispersal/turnover concept, for brevity **the DISTURN principle.** Hence, this principle says: *species can only survive if the investment in dispersal is sufficiently high to compensate local extinctions by sufficient (re)foundings* (den Boer, 1990a). Although carabid beetles gave us the opportunity to prove this principle, of course, it is not restricted to carabid beetles, it applies to all kinds of organisms (den Boer, 1990a,b). .As soon as the possibilities to sufficiently (re)found populations declines natural selection will more favour specimens that do not leave the population area, and thus will gradually reduce the development of wingmusles, reducing wingsizes (den Boer et al., 1980), and changing behaviour that stimulates dispersing. In this way the species concerned will more and more get isolated in the few and often too small remnants of habitat we left to these species in our cultivated countrysides.

In my opinion the DISTURN principle warns us that our habit to reduce the surfaces covered by natural habitats not only directly exterminates many populations of many species, but in a more indirect way also threatenes the survival of other populations of the same and other species that ultimately will get extinct too, because natural selection reduced dispersal from the remnants left by us and thus takes away the natural possibilities of each species to compensate for local extinctions by (re)foundings. The only thing we can still do to somewhat relieve the situation for many species –but not for all, since species with bigger individuals need surfaces we can no longer make available for them- is again enlarging as far as possible habitats. An encouraging example of such a trial is the plan "Goudplevier" of the Dutch Nature Conservation Company "Natuurmonumenten" to interconnect some small remnants of more natural habitat by buying up intervening agricultural fields and letting these develop into a direction that more resembles the situation before reclamation. Such a plan can hardly have been inspired by 'the Island Theory', whereas it would have directly resulted from applying the DISTURN ptinciple.

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Wijster, March 2004