How to study complicated processes under simplified conditions?

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Abstract: It is shown what kind of difficulties a field biologist can expect to encounter when applying the scientific method. He will not only be concerned with simple and direct causal processes, but also with indirect relationships and with multicausal processes. It is emphasized that variability cannot always be considered "stochastical noise" around some expectation value: in many cases complexity and variability have a quite different (e.g. multifactor) structure, and can thus significantly contribute to the stability of the "system" (spreading of risks). By simplifying the environment complicated processes can often be analysed step by step in the laboratory. But we cannot simplify individual organisms, and we can expect to run into difficulties when trying to project our laboratory results at the field situation. Both kinds of difficulties can be circumvented by a sophisticated use of computer simulations combined with field experiments. Field biologists thus will have to move around somewhere between rigorous analyses into smaller and smaller details at the one hand (laboratory), and applying the law of great numbers at the other (overall field data).

We have all been taught that the strength of the scientific method is the ability to show the existence of direct causal relationships. If, for instance, some scientist would for the first time state that water originates from a combination of the gases hydrogen and oxygen, this will have to be considered a hypothesis that ought to be tested, i.e. he has to go into the laboratory, bring together hydrogen and oxygen, and show by sparking over that indeed water is formed (with some explosive noise). Moreover, to be sure that the relationship is a direct one the experiment will have to be repeated several times, and it is expected that each time the result will be the same, i.e. the relationship is not only direct but even deterministic. In this, and in many comparable cases, this expectation will indeed be answered, which means that the bringing into contact of hydrogen and oxygen (with sparking over) is a necessary and sufficient condition to cause water.

Not only chemists, but also biologists work along these lines, and in many cases direct causal relationships can be shown to form the base of many biological processes: e.g. a necessary and sufficient condition to let contract a muscle is to stimulate it electrically; the growing of a maggot into a fly is caused by the taking up of adequate food under the right physical conditions. Note, that the latter addition is a necessary one because at temperatures below zero a maggot will not be able to take up any food. In this case, however, there are still other complications. If under the right conditions a batch of maggots is fed adequately, not all maggots will grow into flies: some will die. Though feeding maggots adequately under the right circumstances apparently is a necessary condition to develop these into flies, it is not a sufficient one.

We will have to add something like: "if all maggots are healthy", but in most cases we will not know exactly what is meant by this (it may mean: if no maggot shows some genetic or physiological defect, but this is not very precise either). We are confronted here with a rather fundamental statistical relationship, i.e. we will have to accept some degree of unpredictability.

In this special case we could possibly try to breed a lot of genetically pure lines of flies in order to find one or more in which all maggots always will develop into flies, but in general biologists will not take the trouble to try this. They have good reasons for that: they are not at all sure, that it will be possible to breed such a pure line. Hence, they accept the variability of living material as an axioma (only geneticists will try to go as deep as possible into the causes of this variability), because they are convinced that the above statistical relationship at the same time is a direct causal one. In cases like the present this is scientifically quite acceptable, I think, but in general we should not a priori suppose a statistical relationship also to be a direct causal one; we will have to exclude all possibilities to attain the same result in some indirect way. And if the investigator posits such a causal relationship as an hypothesis, he is obliged also to describe a feasible experiment by which the hypothesis can be tested unequivocally. The latter addition must be emphasized because too many biologists have the feeling that they have solved a problem, when they have proposed a reasonable hypothesis; they don't care very much about a rigorous method of testing it, or even about its testability at all, and only in a few cases this is acceptable (like in the above one).

To give a not unrealistic example of such an unacceptable case: if some ecologist discovers that over a number of years a significant negative correlation is found between the numbers of some bird species (e.g. the Great Tit) and the numbers of one or more insect species on which the birds are known to feed, he may posit the reasonable hypothesis that the density of the bird is "regulated" by the amount of food available (i.e. by the numbers of these insects) during the breeding season. Such an hypothesis can hardly be tested unambiguously, however, because we cannot make the critical laboratory experiment, whereas in the field we cannot manupilate insect numbers adequately during a number of years and at the same time control all other factors that might influence the fluctuations of density in the birds. The main things we can do, are, sampling the insect species (to roughly estimate densities), studying the breeding succes of the birds in relation to the amounts of food carried to the young, and calculate correlations. But in this way we are not testing some hypothesis on direct causal relations; we are splitting our hypothesis in a number of new ones (Reddingius, 1971), each of which will have to be tested adequately. Moreover, from two independent observations we can rather easily construct another hypothesis that is at least as reasonable (this method of testing examples with counterexamples is a powerful research tool: Reddingius, 1971): During severe winters the mortality of many birds (among which the Great Tit) often is very high, whereas many insects are repeatedly observed to increase in numbers after a severe winter (because of relatively low mortalities in such winters, i.e. independently). Only a few of such winters in a sequence of population counts can be expected to suffice to result in a significant negative correlation between bird densities and insect numbers. Note, that under the latter hypothesis the correlation would result from the coincidence of two quite indepen-

dent causal processes. Such situations are rather common in ecology, cumulating in the practical joke that in many localities over the years a high correlation has been observed between the number of breeding pairs of the stork and the number of newborn childern.

It will be evident that the cited difficulties result from the high level of complexity of the processes involved, a level that can still be grasped by our imagination when breeding maggots into flies, but which cannot be penetrated sufficiently in the case of density fluctuations of birds. In the field situation it not only appears to be the exception rather than the rule to rightly pick out a direct causal relationship, but many quantities in fact do not result from a single cause but are multi-causally determined, which will generally be the case with population numbers, for instance. If a single quantity is the common result of two or more processes, and we study each of it separately as being the process that exclusively determines that quantity, there is a real danger of rejecting each process in turn as not being the "key-factor".

I will illustrate this important question with an artificial example that I owe to Stearns (1982): Most birds that breed over a wide area of the Northern Hemisphere have larger clutches of eggs (and of young) in the northern parts of their area than in the southern ones. Several hypotheses have been proposed to explain this phenomenon, among which 1) higher food densities in the North during the breeding season, 2) a higher chance of predation of especially large clutches (more noise produced by the young birds) in the South, 3) more foraging time in the North because of a longer daylength during the breeding season. We can now imagine two kinds of scientists, a first kind that is convinced that only simple causal relationships do operate in nature (though often embedded in what they

will call "stochastical noise"), and a second kind that reckons with the possibility that a single quantity might result from two or more causal processes at the same time. A scientist of the first kind will collect data on clutch sizes and correlate these with e.g. daylength, because this is supposed to be the causal factor. As he is aware of "stochastical noise" he will present his data in an analysis of variance (see e.g. Sokal & Rohlf, 1969) with the following disappointing result:

Source	df	SS	MS	F
Daylength	1	8	8	2.4 (not
Residual	6	20	3.33..	significant)
Total	7	28		$(F_{0.05} = 5.99)$

Another scientist of that kind adheres the "food-density" hypothesis. He visits the same localities to collect data on clutch sizes and also estimates food densities there. He, too presents his data in an analysis of variance with about the same result, however. He did not pay attention to daylength, because he knew already from the literature that it does not significantly affect clutch size. An adherent of the "predation" hypothesis again attains about the same insignificant results when carefully studying the frequencies of predation of small and large clutches respectively in the different localities. A scientist of the second kind, however, brings together all these data in a 3-way factorial ANOVA with the following result:

Source	df	SS	
Predation	1	8	
Food density	1	8	
Daylength	1	8	
Residual	4	4	
Total	7	28	(interaction terms omitted for clarity)

MS	F	
.8	8	(all 3 are significant)
8	8	($F_{0.05}$= 7.71)
8	8	
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He concludes that clutch size is multicausally determined, i.e. all three factors significantly contribute to clutch size, but only if taken into account all three we can sufficiently "explain" differences in clutch size (none of the causes in itself is a sufficient cause).

Though this is an only artificial example (scientists can hardly be divided rigorously into the above two kinds) it exactly shows what I want to stress: if we study only one cause of a multicausally determined effect the other causes will be condemned to become "stochastical noise" (in an analysis of variance these will magnify the residual term), by which we will underrate the significance of the process studied. Possibly you are inclined to conclude now: "but if the single cause studied already significantly influences the effect we need not worry about other causes that may also be of some importance, because these are - if present - apparently insignificant." This need not be true, however, more than one cause may highly significantly affect the same quantity, as will be shown by Van Dijk in the case of the egg production of carabid beetles (see also: Van Dijk, 1979). The main point is: the predictive value of our reconstruction of reality will be improved, if we are able to include the most important causes in our model. Stearns and Crandall (1981) give an example of this for the circumstances under which natural selection will favour the evolution of delayed maturity. However, such an inclusion of more factors should not become a kind of "curve fitting", i.e. the factors concerned should not be hypothetical constructions but actual determinants. From May (1973) can be learned how important it may be to rightly recognize the actual structure of complexity. He accepts only one (theoretical) kind of stability (also for an "ecosystem"): neighbourhood stability, i.e. the stability resulting from a process that "regulates" in the vicinity of an "equilibrium". Because of this starting point all other processes in his models contribute to some kind of "stochastical noise", by which he could - in my opinion wrongly - show, that the greater the complexity of an "ecosystem" the lower its stability (see also: Den Boer, 1982). Hence, merely assuming that some process will be simply structured, is as dangerous as including a lot of hypothetical factors into a model that should simulate that process. We will return to this.

The above examples will suffice to show that we may expect, that the greater the complexity of a phenomenon studied the greater the chance that it will appear to be multicausally structured (but we should not blindly assume this). Therefore, I suppose that in ecology we have passed a critical threshold: at lower levels of integration we can still solve many problems (but not all) by consistenly applying the scientific method, i.e. looking for direct causal relationships, but in ecology we are predominantly confronted with multifactor effects, which necessitates other methods of analysis in many cases. I will return to this. This not only occurs because individual organisms are highly complex structures, but also - and probably even more so - because under natural conditions the individual is involved in many simultaneously running causal processes, each of which has its own (often complex) structure. This does not mean, of course, that I would advocate the abandonment of the scientific method, and would advice to completely switch over to sophisticated statistical technics such as principal component analysis, cluster

analysis, multiple regression or discriminant analysis. Though such technics can be useful tools to generate interesting hypotheses they are unsuited to actually solve problems in a causal sense. As, moreover, we don't lack hypotheses in ecology, we should primarily develop powerful methods to adequately analyse multifactor processes.

An obvious method to tackle with a complicated situation seems to be: simplifying it to such an extent that it can be studied successfully with the scientific method again. We should realize, however, that each simplification at the same time means: adding one or more assumptions to the base on which rests our hypothesis, and we should not go very far in this, not so far as did e.g. May (1973). As we cannot simplify individual organisms without destroying these, an ecologist can only try to simplify the environment of an organism, i.e. he will study the organism in a controlled laboratory environment. The mathematician can simplify both organisms and environments, but especially the first is not very useful because it can only lead to untestable situations, whereas the latter should be considered with a sufficiently critical attention (as in the case of May, 1973). It is hardly necessary in this company to remark that the method of laboratory experimentation, provided that it is applied carefully and is controlled by an extensive field experience, sometimes indeed will lead to a satisfactory understanding of natural events, but that it may also carry the experimenter from one experiment to another without actually progressing for a long time. In this connection Nelemans will discuss the results of a careful laboratory breeding of *Nebria brevicollis*, which deviate in a surprising way from the expectation, that was based on plenty of field data.

The difficulties with laboratory experiments not always result from keeping constantly environmental

conditions, as could be expected. Andrewartha & Birch (1954: 162) show that the rate of development of the eggs of *Austroicetes* in the field can be predicted with a high degree of precision by interpolating for daily field temperatures between the values obtained in laboratory experiments at different constant temperatures. The temperature reactions of these developmental processes are apparently instantaneous and simply lineair, and this assumption was tacitly accepted when planning the laboratory experiments. Van Dijk will discuss a comparable case for the egg-production of *Calathus melancephalus*. But not always, of course, the influence of variable environmental factors is as easily grasped as in these cases. The egg-production of *Tribolium confusum*, for instance, will increase if the constant temperature is interrupted for some days by a lower temperature: Andrewartha & Birch (1954: 173, Fig. 6.2.1). Especially Thiele (1977) gives many examples where in a fixed period the constant laboratory conditions must be changed in some way to enable carabid beetles to keep their lifecycle in concordance with the course of the seasons. In these and in many other cases the assumption of an instantaneous reaction which shows a lineair relationship with the values of the factor under study is clearly shown to be wrong (or at least incomplete).

Nevertheless, in these respects autecologists generally are in a still better position than population ecologists. The latter can hardly withdraw from possible interactions between individuals in a population and/or from interactions with other organisms, e.g. prey organisms. This highly restricts the possibilities to study population processes under simplified conditions, and thus to rigorously test hypotheses on population processes without starting

from too complicated – and thus often unwarrented – assumptions at the same time. One way to escape from this, is concentrating upon organisms that are supposed to be as simple as the simplified (laboratory) environments in which we should like to study causal population processes. This solution is propagated by e.g. Williamson (1972) who works with micro-organisms in a chemostat. But by such a strategy the difficulties – except for the cases to which it applies directly, e.g. bacteria in industrial processes – are merely shifted to the poor possibilities to reliably generalize the results over other biological populations and/or over other (less simple) environments. This is clearly recognized by Halbach (1979), who studies population processes in relatively simple organisms, rotifers, in the laboratory, and tries to bridge the gap between the simple laboratory conditions and the more complicated natural environments by constructing statistical models that at least allow to predict changes in population numbers in the field. Like Jacobs (1979) he realizes that in the field many different processes may coact to result in the same population number, even in relatively simple organisms. Though the work of Halbach and Jacobs can be considered a significant progress in our understanding of the dynamics of natural populations, it appears still to be difficult to penetrate as far as direct causal relationships. This will especially be a handicap if we work with more complicated organisms, like carabid beetles.

Therefore, Kaiser (1979) proposed another approach that was already practised successfully at Wageningen (Fransz, 1974; Van de Bos & Rabbinge, 1976; Rabbinge, 1976): the individuals approach, the value of which he could demonstrate with Halbach's rotifers. This approach starts from the principle of parsimony (Occam's razor) in that a population is nothing more than a group of individuals, i.e. we should be able to reconstruct population processes by studying individuals (including the reactions of individuals with respect to other individuals of the same group, of course), and then integrating the individual reactions into population processes with the help of simulation models. Such simulated population processes are thus built up from the causal relationships (both uni- and multi-causal), which individuals have shown to keep up with environmental factors (other individuals included), joined again by statistical relationships; the latter being at least needed to account for individual variability and for the heterogeneity of the habitat (e.g. observed differences between interaction groups: Den Boer, 1981), or in a more general sense to account for that part of stochasticity that is unescapably included when working with living material in a natural environment and which results in a certain amount of "spreading of risks" (Den Boer, 1968). Note, that this part of stochasticity is different from "stochastical noise". The test of such models will have to consist in the degree to which these are independently able to predict the fluctuations of numbers in relevant natural populations (and respond adequately to sensibility analyses). Only in a few cases we already reached this level, an example of which is the simulation of the heavy and more or less cyclic fluctuations of the grey larch bud moth in the Upper Engadin (Van den Bos & Rabbinge, 1976). I need not say much more about this individuals approach of population ecology, since at our last symposium at Grieterbusch (Sept. 1978) four students of our group already tried to place their work within this frame. I need only add now, that we are not yet able in this way to reconstruct the fluctuations of population numbers as we observe these at e.g. Kralo Heath, but we

are rather sure that the individuals approach will take us so far.

This brings me back to autecology and to my audience. During many years already we are involved in the autecological processes that determine the chances to survive and to reproduce of separate individuals. In this connection Van Dijk will report about the difficulties -but also about the possibilities- of translating the results of laboratory experiments on the size of reproduction of individual carabid beetles into the amount of reproduction of a field population. He will show that, because of the multicausal character of this process such a translation cannot occur directly, but requires some intermediate steps, i.e. experiments, either directly in the field or by simulation or as a combination of both, in which some conditions can still be controlled and others are dictated by the field conditions.

Though carabid beetles in many respects are especially suited to perform field experiments in enclosures, and thus allow us to form the required link between field observations and the results from laboratory experiments, these experiments also have their own peculiarities, such as complications that originate from the relatively high level of organization of these animals. Most carabid beetles are active predators and thus equiped with rather sensible sense-organs, which particularly influences their behaviour when moving around. We all know that a carabid beetle in a small container will not show a normal walking behaviour, it will continually ran along the edge. In a less obvious way also an enclosure in the field will to some extent affect the walking behaviour: we will have to reckon with a possible "edge-effect". On the other hand, however, we also make use of this effect to attain a high frequency of recaptures of individually marked carabid beetles and thus to follow as closely as possible certain population processes. Baars (1979a) could show that even different kinds of walking behaviour can be distinguished ade-

quately in this way (see also: Rijnsdorp, 1980). But Van Dijk will show, that there are also some inconvenient complications: the "motivation" of the beetle highly determines whether or not it will be caught at the edge of the enclosure. In general, not only the degree of activity but also the walking pattern will be highly influenced by the "motivation" of the beetle: a satiated beetle will be less active than a hungry one, and a beetle that is searching for prey will show a walking pattern that deviates from the "normal" one (Mols, 1979). Therefore, to understand causally differences in walking pattern and in degree of activity it appeared necessary to measure the "motivation" of the beetle. Mols will show that this "motivation" highly depends on the degree of "filling" of the beetle (with food, eggs or fat). At the same time he will show how the relevant causal processes can be integrated into a simulation model which is then expected to predict the degree of activity, some aspects of the walking pattern and even the rate of egg production and deposition. He will thus try to convince you that a simulation model is a useful tool in the study of ecological processes; in the long run it may even be indispensable (see also: De Wit & Goudriaan, 1974).

Don't conclude now, that complexity is a special property of the walking behaviour of active predators like carabid beetles. It is indeed true that the predatory behaviour of carabid beetles is sufficiently complex to make it a hard job to adequately study prey preferences under controlled conditions (a necessary step to get at an understanding of the influence of carabid populations on prey populations). But also the flight behaviour of the related whirligig beetles (*Gyrinus*) appeared to be more complicated than was supposed at first. Van Huizen (1979) showed that the flight of carabid beetles

is highly favoured by certain physical conditions ("nice" weather), but Van der Eijk will show that exposing whirligig beetles to such conditions in the laboratory does not necessarily result in the amount of flight that is observed in the field under comparable physical conditions.

To come to a conclusion: The causal analysis of ecological processes in the laboratory is an indispensable tool in both autecology and population ecology, but because of the multicausal structure of such processes it is a quite different job to integrate the results of such experiments into an adequate picture of ecological processes in the field. Though we can expect still to meet with a lot of difficulties, which will have to be overcome with an appreciable amount of inventiveness, we will have to accept this challenge and not entrench ourselves behind simplifying -and thus often untestable-theoretical constructions. But no more should we blindly go on analysing into smaller and smaller details, for then both the fascinating processes we observe in nature and the beautiful beetles we like to study will disappear for ever. However, where should we have to stop our analyses? It is impossible to give a general answer to this question. I can only conclude that we will have carefully to keep in mind our instruction: contributing significantly to a sound knowledge of natural ecological processes. To arrive there it will sometimes be necessary to go into certain physiological processes of the individual as in the case of Mols, who had to measure the "motivation" of a carabid beetle to understand differences in walking behaviour. Sometimes it will be necessary for this to carefully measure the size of wings and/ or the degree of development of flight muscles, as in the case of Nelemans and as exposed in Den Boer et al. (1980). But sometimes we have to stop already earlier, which I will illustrate with an example. Though it is evident that many different factors both in the detailed structure of the environment and in the walking behav-

iour of individual carabid beetles will significantly influence the chance to be caught in a pitfall, it has appeared unnecessary to study all these events in detail in order to be able to use the number of individuals of a certain carabid species caught in a pitfall as a reliable (relative) measure of mean density: Baars (1979b). Taken over a long period -e.g. the whole reproductive season- these highly variable influences sufficiently cancel out each other to end up in a catch number (summed over that period) that nearly completely depends on the number of individuals present around that pitfall, i.e. on mean density (these influences thus only result in "stochastical noise" around mean density). Hence, if multicausality surpasses a certain threshold it becomes decreasingly payable -and often also decreasingly interesting- to analyse the causal structure concerned, whereas it is warranted to make use of the law of great numbers, i.e. to accept the statistical result together with some degree of unpredictability (stochastical noise). In fact, we already encountered a comparable situation in the first example, the breeding of maggots into flies, where we had to accept the variability of living material. Note, however, that this case in sofar is different in that the amount of maggots dying cannot be considered "stochastical noise" around the expected outcome of the causal developmental process.

But again we are confronted with the question: "When should we continue our analyses, and when should we have to make use of the law of great numbers?", and again I cannot give rule for that. However, I am sure that a skilled ecologist, who is not content with a few inscrutable correlations but who wants to know how the more important ecological processes are actually structured, will know this by intuition. But what is intuition? Intuition is the result of multicausal processes, that in my opinion are worth to be

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analysed, if possible.

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