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Commentary

Strict statements and their consequences — a story around cycles

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The polymorphic-behaviour hypothesis alias Chitty hypothesis has been a very characteristic element of the evolving theoretical population ecology during the second half of the 20th century. This paper considers the origins and fates, among the scientific community, of the ideas upon intrinsic regulation of population fluctuations through balanced, especially behavioural, polymorphisms. The final formulation — presumably quite independently in separate quarters — of such ideas into hypotheses identical as to their conceptual contents has been examined. The maturation of the hypothesis into a conceptually unambiguous form advanced very differently in step, however, in separate quarters. This, in turn, interestingly disclosed how such a difference can be based on differences in the interests or training of the pertinent authors in the special fields of theoretical population biology. The vicissitudes of the concept in the writings of several eminent population ecologists before and after the well-known extensive period of painstaking efforts to test the polymorphic-behaviour hypothesis have also been surveyed. It appears that ideas upon genetic mechanisms associated with cycles have continued in the treatises of population biologists through the 1980s until the present. This can be interpreted as a first rate indication indeed of how difficult it really is to imagine a population strongly fluctuating with cycles that would not possess any kind of intrinsic strategies specifically adopted for readiness to resist alternatively repeating stresses of different origins.

1. Origins and fates of hypotheses on intrinsic regulation of population cycles

If one reads a paper on population dynamics and comes across one or more expressions like intrinsic mechanisms, natural selection, viability, or behaviour of individuals, he or she will be certain that its author belongs to the "intrinsic regulation of population"-school. While such papers have been and still are common, there are ecologists who claim that thinking along such lines is obsolete.

Considering what has occurred in population ecology during the last three decades, such statements, though understandable, are badly exaggerated, if not simply wrong in certain respects at least (Voipio 1988). The treatise mentioned has its predecessor (Voipio 1978). It was intended, principally, to emphasise the genetic variation seemingly associated with population dynamics, and to stress the intimate relationship of population ecology with population genetics. The paper is a continuation of my early treatises on cycles

(Voipio 1950ab), and was based on an invited lecture for the Theoretical Biology Seminar ordered by the Finnish State Council for Natural Sciences in December 1977.

The latest of the treatises mentioned (Voipio 1988) led to unexpected consequences, seemingly because it indicated the particulars of the development of the ecogenetic outlook in the writings of the population ecologists, including myself. I had been well aware of the fact that my earliest papers (Voipio 1950ab) dealing with the possibility of intrinsic regulation of the populations of the cyclic species had been overlooked in the ecological literature. Such was the case in spite of the positive reviews by Francis Evans (1951) and Ernst Mayr (1952) in *Journal of Wildlife Management* and *Evolution,* respectively. Though not referring just to the cycles, both rereviewers took notice of my view of the synthetic population biology, viz. the intimate connections between population ecology and population genetics.

Considering the causes of such a fate, the following circumstances may have been of importance: (1) a poorly known forum (periodicals for game research and management), (2) an outlying country compared with those with important scientific centres at that time, and (3) hesitation among ecologists to accept such views in the early fifties.

It was a positive surprise, thus, that Stenseth and Ims (1993) brought them up in their survey of the history of the studies on microtine rodents and stated clearly that intrinsic factors associated with genetic (and even with behavioural) processes were seriously considered in them as important elements in population dynamics of the cyclic species.

Besides this as such positive tenor, their remark contained, in a sense, also a negative element when they took a stand in the chronological order of the relevant publications. When writing my early treatises (Voipio 1950ab) I knew, besides Charles Elton, several authors, mainly geneticists, whose papers dealt with problems related to population dynamics in some way or another. In the paper (Voipio 1978) which followed (barely 30 years later), the situation was quite different of course. Among citations referring to the relevant publications, those referring to Chitty (1960, 1967) and Wellington (1960) were of key importance now. These authors, in fact, were the core of workers emphasising the association of genetic variation with population dynamics and its potential importance to the mechanisms of a populations' self-regulation.

I have been clearly aware of my fate of being ahead of some others, not only in chronology, but also in regard to the scope as to the contents of the theory itself. But I had no need to voice it abroad. I felt myself to be some kind of arm-chair ecologist, compared with those working hard in equally hard field and lab conditions. In the treatise of 1978, I referred to my earlier papers in passing only, with the remark, to be sure, that because fluctuations in number seemingly contained mechanisms in which population dynamics and population genetic phenomena were coupled somehow, the members of populations presumably were harmoniously adapted to their strongly varying alternating conditions by means of physiological polymorphism(s).

As for, finally, the latest treatise (Voipio 1988), it would have been rather strange had I not mentioned my own participation in the discussion on cycles. And from this, in fact, it followed that Stenseth, in the capacity of referee, automatically provided the chronological order of the pertinent publications of the two authors, Dennis Chitty and myself. It is not a question of priority (a trifle in science itself), what matters is the contents of the statements by Stenseth (1933: 11), the gist of which is not only speaking upon "similar ideas" but, particularly, specifying the identity of the hypotheses as to their contents. A fine confirmation for this is to be found in Chitty's recent wonderful and thought-provoking book (Chitty 1996: 137).

One question still remains, viz. that of why the hypotheses (widely accepted later and epitomised as the Chitty hypothesis) ripened and matured to a clearly identifiable hypotheses out of step? I remember asking myself the question then, and being well aware of Chitty's continuous advancement towards a tight hypothesis, but could not find an explanation. However, I think I have solved the problem now, and with the help of Chitty's own work. The key can be found on page 136 of his book where he writes: "I could not have given this paper [Newson & Chitty 1962] without … Janet's knowledge of population genetics and haematology". This shows clearly that Chitty thought in terms of genetics and natural selection and stated that "cyclic declines occur if and only if preceded by natural selection" (Chitty 1996).

This is the point. The difference between us seems to have been that I chanced to be, contrary to Dennis Chitty, moderately well trained in theoretical population genetics (Voipio 1950a) already from the beginning of my career. In my thesis work just mentioned, genetic polymorphism was instrumental and actually served as a lead theme throughout the work with specific application in treating cycles (Voipio 1950ab), not only in terms of physiological polymorphism with varying viabilities at different stages of the cycle, but also in terms of genetically determined behavioural (migratory or dispersal) morphs (see below).

2. Behaviour as an element of hypotheses concerning cycles

As the behaviour, according to the hypothesis, constitutes a part of the intrinsic mechanisms of the cycles, it may be worth considering the papers of a couple of workers objecting to the view of intrinsic regulative factors.

The essence of their thought is briefly as follows: "The changes in aggressive behaviour … to block breeding by the hypothesis of genetic-behaviour polymorphism do not occur" (Laine & Henttonen 1983: 409) and "Social regulation, based on genetically polymorphic behaviour, seems to be in principle unable to create population cycles" (Henttonen *et al.* 1986: 4).

Considering what had been written about the behaviour of the microtine rodents subjected to cyclic fluctuations, not only up to then, but also during the subsequent years, such assertions are at least as provocative as those concerning the mere intrinsicalness of regulation.

It is because of this behavioural element that Chitty (1996: 23) favours the term "polymorphic-behaviour hypothesis" before the "Chitty hypothesis". His argument for this is, firstly, that "It's uncertain which stage of an evolving explanation should be so labelled", and, secondly, that "Voipio proposed a genetic explanation long before I did". While agreeing with the former, I would like to emphasise that my proposal indicated also, and implicitly, that the structure of this hypothesis is twofold and raises the interesting question of when or at what stage of the evolving explanation the behaviour element ultimately entered into its conceptual framework.

It seems to me that presenting the "preconceptions inevitable at a new stage of work" based on "the only positive evidence that it [the cause of the population decrease] might be invariably related to mutual interference" (Chitty 1957) clearly indicates the core of his idea, viz. the significance of the properties of individuals with different selective advantages at different phases of the cycle. Such words as "polymorphism" and "behaviour" are still absent, but the idea of polymorphism is quite evident, however, though related to haemolytic anaemia, not just to any specific behavioural factor.

Developing his ideas further (Chitty 1960), among other things by relating behaviour with dispersal, Chitty (1967) eventually takes a great step not only by associating behaviour with dispersal but also emphasising that "this behaviour *persists* only because it has survival value for the individual and is *constantly* selected for" (thus representing some kind of polymorphism; italics mine, see also Chitty & Phipps 1966). Though he expresses some hesitation by stating (Chitty 1967: 62) that "the idea that behaviour might be polymorphic is too *recent* [my italics] for us to know how fruitful it will be", he compensates by speaking (in the summary) of "the selective advantage of the supposed behavioural polymorphs" — for the first time in this combination of words.

Opinions of when the Chitty hypothesis actually appeared in its final form, i.e. as an unambiguous biological concept, have differed considerably. Most of the authors regarded the 1967 treatise as *the* paper of foundation. I agree, though with the mildly heretical thought that the concept actually appeared in its ultimate fashion, viz. as an epitomised "polymorphic-behaviour hypothesis" three years later (Chitty 1970). The hypothesis thus matured, demonstrated its essential elements unambiguously and briefly.

But what are the fates of the concept of behavioural polymorphism in the writings of other ecologists? One of the earliest was Andrewartha (1959) who was led to the assumption that the mechanisms of the matter *must* be polymorphisms maintained by specific genetic processes: "it would be reasonable to look for some form of balanced polymorphism [N.B] in any population that shows territorial behaviour, or even more generally, in any population that shows some other form of self-regulating mechanism" (l.c. p. 205). I received this paper from its author with the heightened pleasure because it was not only one of the earliest papers in which an ecologist presented such views, but it was also the first time, since the beginning of the 1950s (Voipio 1950ab), that the possible role of genetic factors had been emphasised in terms of "balanced polymorphism".

I was also impressed with Andrewartha's paper simply because I myself had proposed not only that "certain individuals, when the stock collapses, survive better than others" (Voipio 1950b: 71) but also that they represent different types of behaviour due to which "natural selection will favour, depending on occasions, as well the resident behaviour as the migratory tendency as a factor controlling population density" (Voipio 1950a: 163).

It was, thus, of great interest that Lidicker (1962) presented, three years after Andrewartha's paper, a treatise centring in the behavioural element of the population dynamics of the cyclic species. His argument resulted in a genuine polymorphic-behaviour hypothesis. I greeted it with enthusiasm (*see* Voipio 1978: 32) as a "novelty" in the ecological literature. The treatise culminated in the following words: "a genetic balance (possibly polymorphism) would develop between the perfection of responsive emigration tendencies, with its attendant selective advantages, and the tendency to be sedentary and to stay safely at home, with all of its attendant selective advantages" (Lidicker 1962: 31).

3. Belief in intrinsic mechanisms continues

It is well known that a long period followed during which the polymorphic-behaviour hypothesis was submitted to painstaking tests elaborated by a group of research workers well suited to be called the Chitty/Krebs school. It ended with results not supporting the Chitty hypothesis — but only in respect to genetic variation, related to electromorphs having been revealed through investigations on allozymic variation. In terms of the art of modelling, the "theory did not allow formulation of models for demonstrating its plausibility", according to the parlance of Stenseth (1977). I, for myself, concluded that the "truth evidently lies in the interaction between (perhaps rather specific) an extrinsic factor or factors, and intrinsic factors with a large number of potential regulative functions" (Voipio 1988: 331).

Though the situation appeared rather fatal for any hypothesis on intrinsic regulation, my conclusion was formulated with an intentional emphasis on the very vagueness of inferences denying any possibility of genetic factors in regard to both the intrinsic factors in general and the behaviour associated with them in particular.

In the following, I refer to some expressions of certain authors which reflect their thinking in terms of alternating selection regimes. Haukioja (1980), for example, wrote: "genetic changes in herbivore populations during cycles are almost inevitable because selection pressures must differ at different phases of the cycles due to varying levels of plant defences". This indeed is the idea which has engaged the minds of the research workers continually. So, for example, Williamson (1972: 91) reasoned that "interaction of genetics and ecology are [sic!] thought to be essential" when recurrent demographic situations create conditions sufficient for alternate selection, so preparing the way for a strategy based on response-to-selection polymorphism.

Ideas on polymorphic behaviour continued in the subsequent works of the population biologists through the 1980s (Voipio 1988). The weightings had changed considerably: suggestions on genetic factors not as a sole cause of cyclicity appeared. But emphasis on various grounds of intrinsic factors existed side by side with the new doctrine of interaction between exclusively extrinsic, biotic and abiotic, factors of which the predators should possess the central role.

The 1990s seem to be no exception. Lidicker (1994), for example, having abandoned his earlier belief (Lidicker 1962) in the polymorphic behaviour, wrote as follows: "The intrinsic–extrinsic dichotomy is now generally accepted as a non-issue" that is, "the diversity regulation machinery consists of the organism–environment axis and not with either component alone". It is to be noted that emphasis upon "multiple-factor perspectives" does not abandon the view of even numerous intrinsic factors interacting with the extrinsic ones during the cycle. Among the former, as Lidicker argues, certain characteristics of the dispersal behaviour are suited to indicate that "at least some dispersal is favoured by natural selection".

This holistic approach notwithstanding several authors from the late 1980s and early 1990s continue to think of the problems in terms of genetic processes as ultimate factors maintaining cycles. This can be seen from several treatises dealing with microtines (Desjardins *et al.* 1986, Boonstra & Boag 1987, Tamarin & Sheridan 1987, Spears & Clarke 1988) and tetraonids (Moss & Watson 1991, Watson *et al.* 1994) as well as certain insects such as lepidopterans and moths (Mitter & Schneider 1987, Baltensweiler 1993).

In all of these studies their authors have either assumed genetic mechanisms correlated with population cycles and, thus, being worth studying, or simply disclosed such genetic variation that possibly or probably could be of importance. It may be appropriate, in this context, to call to mind Stenseth's (1981, 1985) analyses of Chitty's hypothesis because there is some similarity between his theoretical modelling and the considerations of mine upon polymorphisms presumably operating in association with cycles.

The important point in these analyses is the issue that two genetically determined behavioural types, e.g., docile and aggressive, are not likely to give rise to any cyclicity in an extrinsically stable environment. They do that, however, if some extrinsic non-biotic factor influences the population through the quality of individuals. The interaction between intrinsic and extrinsic factors can then work as a cause for cycling (*see* Voipio 1988: 329) thus giving some plausibility to the Chitty hypothesis. But Stenseth proceeds further when he asks whether *poly*morphic, instead of *bi*morphic, differences could bring about fluctuation in cycles. As he points out though, such models have not been analysed, to say nothing of analyses of populations with three or four phenotypes (with nearly insurmountable difficulties to study) they would be important for assessing the plausibility of Chitty's hypothesis.

It is here that I see the (concealed) similarity between Stenseth's analysis and my considerations concerning the polymorphic basis of the population cycles. I argued, namely, from the first (Voipio 1950a: 163) that a cyclic population cannot manage on the basis of one polymorphic system alone, but that more elaborate polymorphic systems must be functioning during fixed but different phases of the cycle. This means that "these different phases represent situations in which not only the demographic parameters vary but the extrinsic factors (abiotic or biotic) relating to weather, grazing or parasites are also at work with corresponding polymorphic strategies of their own."

To summarise, one simply cannot imagine a population fluctuating with great amplitudes and deep lows, and experiencing great repeated changes in their environment involving diseases, predators, food shortages, social interactions and so on that would not possess appropriate strategies specifically adopted for several kinds of environmental stresses confronted with at different phases of the cycles.

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