

Commentary

A story around cycles — a commentary

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Since the 1920s, ideas on population cycles of small rodents and hares have circulated around, although the first comments on regularity in lemming dynamics were made by Finnish zoologists already in the 1850s (reviewed by Henttonen & Kaikusalo 1993). As it often happens in science, ideas prevailing and being remembered center in the Anglo-Saxon world. Voipio's early papers (1950ab) serve as a prime example of how important ideas can be forgotten if published too early in relation to the conceptual environment of the time, or in a local journal in a small country, or as in Voipio's case, both. Fortunately, the latter statement is not always universal; e.g., Kalela's (another Finn who studied population cycles) early papers (e.g., 1957) received a lot of attention, and are still often cited.

Why, unlike Kalela, was Voipio forgotten, even though his papers were immediately and visibly reviewed? I would be inclined to say that Voipio's ideas appeared too early in many respects. In the 1950s, physiological stress interacting with climate, and density dependent social constraints were the prevailing hypotheses (Frank 1957, Kalela 1957), even with some ingredients of group selection. Voipio's idea on cyclic variation in general adaptedness, based on genetic and physiological polymorphism, was obviously far beyond the main thinking of that time. Furthermore, the main trend of the time was empirical, and as Voipio (1998) himself proudly states, he was an arm-chair ecologist, a breed well-known today, but not at

the turn of the 1940s and 1950s. Finally, in the early 1950s, no methods were available, neither genetic nor statistical, to test Voipio's ideas.

Chitty's ideas on the causes of population cycles developed step by step in the course of decades towards what is now known as the Chitty hypothesis or the genetic-behavior polymorphism hypothesis (Stenseth 1977, Chitty 1996, Voipio 1998). As Voipio points out, a kind of polymorphism thinking could be seen in Chitty's papers already in 1957, but not until 1967 were the genetic polymorphism, and natural selection clearly involved. Chitty published his 1967 and 1970 papers unaware of Voipio's early work. However, in his recent book, Chitty (1996) gives a beautiful credit to Voipio's early ideas on genetic polymorphism. On the other hand, it is a bit surprising that in his book Chitty does not refer to Kalela at all.

If one wishes to compare Voipio's and Chitty's ideas on genetic polymorphism, it is clear that Voipio's approach was more holistic. While Chitty discussed aggressive and docile genotypes, and their relative changes in different phases of the cycle, Voipio understood the cyclic polymorphism at the level of genetically based physiological processes as a whole. On the other hand, it is clear that Chitty's narrower approach was more testable than Voipio's arm-chair ecology.

Personally, I feel very happy that Paavo Voipio, now in his mid-80s, has received the merit he deserves, and can still enjoy it. I have also a personal reason for this satisfaction. When Stenseth

and Ims (1993a) edited *The biology of lemmings*, which included an article on the history of microtine cycle research (Stenseth & Ims 1993b), I reminded them in my review of Voipio's early papers, and also a later one (Voipio 1988). As a result, his papers were included in their text. Chitty obviously read about Voipio's ideas from the 'lemming book'. Somewhat later, I happened to meet Paavo Voipio in the Department of Zoology of the University of Helsinki (now Division of Population Biology, Department of Ecology and Systematics), where he had, and still has, a small but active emeritus office after his retirement from the University of Turku. On that very same day, Voipio had received a letter from Chitty. It was a very polite letter, the best of Chitty's well-known style, where he acknowledged Voipio's early work and regretted not having known it before. Chitty promised to give full credit to Voipio in his forthcoming book, as he did. Voipio seemed a happy man.

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