Rejoinder

Peter Jagers

In his famous deduction of the motion laws in an ideal gas, Maxwell showed that if velocities in the three base coordinates are independent and identically distributed and their joint frequency function is determined by the kinetic energy, then the velocities must be normally distributed. This is an unusual case: Idealized, but not ridiculous, assumptions determine a parametric family of standard distributions. More frequently it is mathematical convenience that dictates the assumption of the most popular special distributions: exponential or deterministic life spans, Poisson reproduction, Brownian migration, special laws of neighbor interaction, to quote some examples from population dynamics or particle systems. The rationale might then be either the hope that the ensuing results should have a more general validity than for the special case in which they have been deduced or that the special assumptions made are "natural" in some yet unproven sense, or, possibly, that the resulting mathematics is beautiful enough to warrant the work.

The general branching process approach to population dynamics, which I have tried to sketch, belongs to another tradition. No assumptions about special distributional forms are made, and results are obtained through general mathematical and probabilistic laws, like the law of large numbers. This, of course, yields a much greater applicability of results, and we can feel more secure that the claims made are not based upon some incidental property of, say, the exponential distribution. But there is a price to be paid: Many topics cannot be investigated in this general setting.

In particular, this concerns interaction properties, like those in genetics, or of spatial interaction. Nevertheless, I like to see branching process on the track toward more and more interdependence, along similar lines as the classical analysis of sequences of random variables has developed. In this spirit, I described Galton-Watson processes as the theory of sums of iid random variables on trees, and multitype processes as the theory of summation of Markovian random entities on trees. A natural continuation of such a program would be to consider other concepts well known for sequences of random entities for entities defined on trees, from m-dependence and mixing to ergodicity. The case of sibling interaction has already been treated (Broberg, 1987), and work is under way on more general interaction that is local in the family tree.

I believe that Cohen's remark about unobserved heterogeneity and partially observed Markov chains should fit well into such a research program (even though his opening remarks about Markovianness have to be taken carefully, since not even in his simple case size and composition over types constitute a Markov process in real time). Cohen's second suggestion, to join together random mating with population growth models, is nice. One should only realize that random mating forces a rather simplistic age structure on the population growth model, much as in Cohen's own example. This is one of the areas where the general type of modeling I have advocated above seems to fall short.

The independence assumptions, that are clearly the weak point of branching processes, are also taken up in Sawyer's comment. Here it is the interaction between the population as a whole (carrying capacities) and individual reproduction that are pinpointed. Again, I believe that there is little hope to solve such problems without the assumption of special distributions. The most general results I know of concern Galton–Watson and birth-and-death type processes (Klebaner, 1989, and earlier papers).

Donnelly's comments give a succinct description of the structure of genetics models. I am particularly grateful for the carefully phrased and nontechnical discussion of the molecular clock hypothesis. If there is anything for me to add, it is only to underline that this is a discussion in terms of the traditional genetical models. Of course, this is the framework in which the hypothesis was first formulated and is usually discussed. However, it is only a model, depicting some aspects of reality acceptably well, others with rather much of contortion. Like Sawyer, I find it comforting if the hypothesis and therefore also related entities, like Donnelly's k_a, the rate of evolution along an ancestral line, or u, the rate at which mutations occur to an individual, turn out to appear naturally in branching processes as well. If $k_a = u$ always in the context of population genetical models, but only under added conditions in branching models, it is natural to check whether these extra assumptions are implicit in population genetical models and to what extent they seem to be valid in reality. The formation and testing of the molecular clock hypothesis in various models is an important part

of testing its validity beyond particular models (a point that is certainly clear to Sawyer and Donnelly, but may be not so to the most ardent proponents of the molecular clock!).

Let me end by thanking the discussants for their comments, and also the editor for a choice of discussants, supplementing my own background in branching processes with distinguished representatives of other traditions within population dynamics.

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