

To understand the way the theory of large fluctuations works, one must picture all the possibilities of a system's motion. These can be represented as paths in a mathematical phase space (Fig. 2). Each path the system might take can be assigned a particular probability density, related to a mathematical quantity called the 'action'. The probability decreases very sharply as the action increases, and the rate of occurrence of very rare events is determined not by all possible paths, but with overwhelming weight by the most probable, or optimal path, and a narrow 'tube' of trajectories about it. Thus many important problems can be reduced to ones involving an analysis of just one dominant path. Luchinsky and McClintock's study¹ is an important step in assessing the reliability of these theoretical ideas to real-world situations.

The authors were able experimentally to study models originally suggested by theorists to illustrate several types of nonequilibrium behaviour. What made this possible was the clever trick of doing electrical analogue simulations of the systems. In this way the relationships between the theoretical objects and experiment can be demonstrated very cleanly. However, data from 'real' experiments may still be a somewhat remote prospect. Although the optimal paths are

observable, Luchinsky and McClintock's simulations sometimes required data to be collected for as long as a week.

Whereas the behaviour of equilibrium systems is 'smooth', large-fluctuation treatments of nonequilibrium systems^{2,3} give rise to singularities — places where behaviour changes suddenly. Opinions varied as to what these singularities signified, and some researchers asserted that the method of large fluctuations simply was not valid in such cases. But in recent years a topological analysis of optimal paths (Fig. 3) has proved that the physically important singularities can be understood within the framework of the theory of large fluctuations⁴.

What excites researchers is the wealth of new and unexpected phenomena related to these singularities. An example is the way the optimal path in a system such as a nonequilibrium chemical reaction can suddenly change shape⁴⁻⁶, leading to a 'kink' in the plot of reaction rate versus some parameter^{5,6}. This is a result that is sharply at odds with the 'escape rates' of a system in equilibrium⁷, the basis for understanding chemical reactions and similar phenomena for the past half century.

This emerging topological viewpoint is analogous to the viewpoint of chaos in nonlinear dynamical systems. As Poincaré

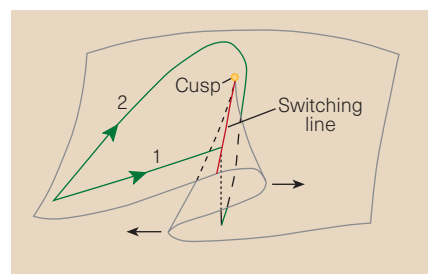


Figure 3 Switching in nonequilibrium systems. As some physical parameter is varied, the sheet on which the optimal path lives (in an abstract mathematical space) can fold over. The further from equilibrium the system gets, the greater the chance that such folds will develop. The optimal path to points on one side of the switching line is direct (path 1), whereas the optimal path to points on the other side of the switching line must detour all the way around the cusp point of the fold (path 2). The switching of optimal paths that arises with the appearance of the fold can lead to a sudden change in the behaviour of the system.

realized near the turn of the century, the dynamics of nonlinear systems are often far too complicated to be comprehensible by ordinary analysis. He suggested that the way to understand such systems was through a study of the geometric patterns of their

Avian sex-ratios

Pretty Polly, Polly, Polly, Polly, Polly ...

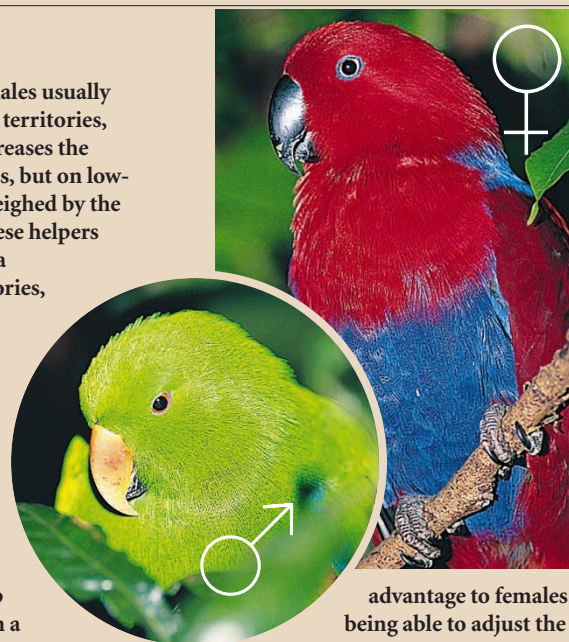
Most organisms produce roughly equal numbers of male and female offspring and, many years ago, R. A. Fisher proposed the explanation for this — in a population in which one sex predominates, the members of that sex will produce fewer offspring (on average) than will those of the minority sex. So, genotypes that produce more of the minority sex than the population average will be favoured.

There is increasing evidence that some female birds control the ratio of sons to daughters in their families^{1,2}. The latest example is reported by Heinsen *et al.*³ in this month's *Proceedings of the Royal Society*. The authors found that most eclectus parrots (*Eclectus roratus*) produce long runs of offspring of one sex — one female produced 20 sons in succession, followed by a run of 13 daughters.

Avian sex-ratios may depend on the position of an egg in the laying sequence, the date of breeding, maternal age, and the sexual attractiveness and condition of the father². Before the new study, the most extreme variation in sex allocation in birds was shown by the Seychelles warbler, *Acrocephalus sechellensis*⁴. In this species, young females often remain on their parents' territories and help to rear subsequent offspring (cooperative

breeding), whereas young males usually move away. On high-quality territories, help from the daughters increases the parents' reproductive success, but on low-quality territories it is outweighed by the amount of resources that these helpers consume. So, daughters are a disadvantage on poor territories, and only 13 per cent of offspring produced on such territories are female, contrasting with 77 per cent on good territories.

The Seychelles' warbler story is relevant to the new study because — uniquely among parrots — *E. roratus* is also a cooperative breeder, with up to ten males associating with a single breeding female (or, sometimes, with one or two other females). Unfortunately, the natural history of the species is poorly known. Moreover, the sex-ratio results were based on the records of aviculturalists, who keep the birds in traditional pairs. These are so different from the natural breeding system that they do not provide clues as to what determines sex-ratio adjustment. One can only speculate that, in nature, there is an



advantage to females in being able to adjust the sex of their offspring in relation to the relative numbers of males and females in the breeding group.

Jeremy J. D. Greenwood

Jeremy J. D. Greenwood is at the British Trust for Ornithology, Thetford, Norfolk IP24 2PU, UK.

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