Chaos in a cup of flour

More than 20 years ago, theoretical ecology was instrumental in stimulating widespread interest in non-linear dynamics and chaos[1,2]. Since then, the existence of chaos has been demonstrated in fields as diverse as fluid dynamics[3], planetary orbits[4], optics[5], physiology[6] and animal behaviour[7]. Ironically, chaos in population ecology remains controversial.

The theoretical developments pioneered by May[1,2] have inspired many attempts to identify chaotic fluctuations in real ecological systems. Many sophisticated techniques have been employed to analyse observed time-series of population abundance, but these studies have so far been inconclusive[8,9]. This is primarily because the available ecological time-series are too short to detect chaos unambiguously; in addition, the data are influenced by external stochastic noise and measurement errors, which may masquerade as chaos in short time-series. So, although ecological systems often have properties that can generate chaos in principle (high mortality in dense populations and rapid growth when densities are low), there is, as yet, no specific system that is generally accepted as showing chaos[10]. Consequently, some have looked for evolutionary forces that would drive population dynamics away from the chaotic regime[11]. Although some theoretical investigations have indeed predicted evolution towards dynamical equilibrium[12,13], others have shown that natural selection can favour, in principle at least, chaotic dynamics[14,15].

Chaotic fluctuations can also be sought in the dynamics of laboratory populations, where environmental noise can be controlled and, if the study organism has a short generation period, relatively long time-series can be obtained. Here, we report on the recent findings of Costantino and colleagues[16–18], who have carried out long-term laboratory experiments on the population dynamics of the flour beetle *Tribolium castaneum*. In these experiments, beetle populations were maintained in containers of flour; every two weeks, the flour was replaced and the numbers of adults, pupae and larvae were censused. In unmanipulated trials, population densities converged to an equilibrium, so in order to explore the possibility of more 'interesting' dynamics, Costantino *et al.* experimentally varied some demographic parameters (such as adult mortality or adult recruitment rate) during the census period. The experimental results were then contrasted with the dynamics predicted by a relatively simple mathematical model of their system[17].

The findings of Costantino *et al.* are interesting on at least three grounds. First, they show how effectively an appropriate mathematical model can predict transitions in the dynamical behaviour of a real ecological system, albeit in the laboratory. The most impressive feature here is that the same model can correctly predict system behaviour under very different environmental conditions. Second, their populations appear to exhibit a broad range of dynamics, from equilibrium stability to two-point cycles, quasiperiodicity and chaos[16–19]. Third, their system shows chaotic fluctuations within very reasonable bounds, providing empirical evidence for the theoretical possibility that chaos need not necessarily increase the risk of population extinction by driving densities to extremely low levels. This has been a recurring criticism of chaotic population models[11].

The work of Costantino *et al.* represents significant progress, but some may argue that their data do not yet provide an unequivocal example of chaotic dynamics in a laboratory population. It would be valuable to explore this interesting system further, in order to establish with greater certainty the agreement between their model predictions and experimental observations. One technique could be to use a number of different starting densities for the experiments, which would unambiguously demonstrate convergence to an attractor. More importantly, a statistical measure is needed to confirm that the attractor that the populations reach is in fact the same as that predicted by the model.

Costantino *et al.* have shown that progress on fundamental issues can be achieved by a truly inter-disciplinary collaboration between experimental ecologists and theoreticians. Their results also highlight the possibility of 'coercing' populations into exhibiting specific, and at times exotic, dynamics. This has obvious implications for conservation and management programmes.

As ecologists, we are interested in explaining observed patterns of fluctuations in natural populations. Valuable lessons can be learned from the behaviour of ecological systems that are artificially exposed to specific conditions. It is hoped that this approach will reveal underlying mechanisms that control real populations, exposing the circumstances under which particular dynamics might be expected. Costantino *et al.* have taken an important step in this direction.

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