dergo conventional multicomponent phase separation, the dominant order parameters for the observed L-L phase change were the density and entropy of each melt phase. Here, the melt passed through the glass transition and the L-L phase transition almost simultaneously, allowing both of the (metastably) coexisting liquids to be quenched and studied in the glassy state.

Liquid polymorphism has also been reported in the organic liquid triphenyl phosphite (*13*). Indirect evidence for liquid polymorphism can also be found in studies of the conductivity of certain molecular liquids, such as I, Se, and S (*14*). During compression, abrupt increases in the conductivity have been observed and attributed to first-order L-L transitions. The L-L transitions attributed to the melt phases of Si, Ge, and C are also predicted to occur with large changes in conductivity (*15*).

These findings indicate that liquid polymorphism in systems with fixed composition is an observable phenomenon and that further candidates will be uncovered as we probe more deeply into liquid behavior over a wider range of pressure-temperature conditions. The occurrence of L-L transitions can lead to the synthesis of new, technologically useful families of liquids and glasses chemically identical to currently known substances but with quite different thermodynamic, rheological, and other physical properties. Also, the complex behavior of viscous liquids and the nature of the glass transition itself are recognized as important, unsolved problems in condensed matter physics (*16*). The occurrence of liquid polymorphism in low-temperature liquids might be one source of this complexity. Recognition and study of L-L transitions should therefore both enrich and illuminate the phenomenology of the liquid state at low temperatures.

An enhanced version of this Perspective, with live links, can be seen in *Science* Online on the Web at http://www.sciencemag.org/

References

1. A. F. Wells, *Structural Inorganic Chemistry* (Clarendon, Oxford, 1984).
2. H. E. Stanley, *Introduction to Phase Transitions and Critical Phenomena* (Oxford Univ. Press, Oxford, 1971).
3. A. C. Mitus, A. Z. Patashinskii, B. I. Shumilo, *Phys. Lett. A* **113**, 41 (1985).
4. E. P. Donovan, F. Saepen, D. Turnbull, J. M. Poate, D. C. Jacobson, *J. Appl. Phys.* **57**, 1795 (1985).
5. W. D. Luedtke and U. Landman, *Phys. Rev. B* **37**, 4656 (1988); C. A. Angell, S. Borick, M. Grabow, in *Proceedings of the 17th Conference on Liquids and Amorphous Semiconductors*, in press.
6. O. Mishima, L. D. Calvert, E. Whalley, *Nature* **314**, 76 (1985); O. Mishima, K. Takemura, K. Aoki, *Science* **254**, 406 (1991); O. Mishima, *Nature* **384**, 546 (1996).
7. H. Sugiura, K.-I. Kondo, A. Sawaoka, in *High-Pressure Research in Geophysics*, S. Akimoto and M. H. Manghnani, Eds. (Reidel, Dordrecht, 1982), p. 551; M. Grimsditch, *Phys. Rev. Lett.* **52**, 2379 (1984).
8. K. H. Smith, E. Shero, A. Chizmeshya, G. H. Wolf, *J. Chem. Phys.* **102**, 6851 (1995).
9. G. H. Wolf *et al.*, in *High-Pressure Research: Application to Earth and Planetary Sciences*, Y. Syono and M. H. Manghnani, Eds. (American Geophysical Union, Washington, DC, 1992), p. 503.
10. P. H. Poole, F. Sciortino, U. Essmann, H. E. Stanley, *Nature* **360**, 324 (1992); F. Sciortino, P. H. Poole, U. Essmann, H. E. Stanley, *Phys. Rev. E* **55**, 727 (1997).
11. H. E. Stanley *et al.*, *Physica A* **205**, 122 (1994).
12. S. Aasland and P. F. McMillan, *Nature* **369**, 633 (1994).
13. A. Ha, I. Cohen, X.-L. Zhao, M. Lee, D. Kivelson, *J. Phys. Chem.* **100**, 1 (1996).
14. V. V. Brazhkin, R. N. Voloshin, S. V. Popova, A. G. Umnov, *Phys. Lett. A* **154**, 413 (1991); *High Pressure Res.* **6**, 363 (1992).
15. A. Ferraz and N. H. March, *Phys. Chem. Liq.* **8**, 289 (1979); E. G. Ponyatovsky and I. O. Barkalov, *Mater. Sci. Rep.* **8**, 147 (1992); M. van Thiel and F. H. Ree, *Phys. Rev. B* **48**, 3591 (1993).
16. P. W. Anderson, *Science* **267**, 1615 (1995); A. P. Sokolov, *Science* **273**, 1675 (1996).

POPULATION BIOLOGY

Chaotic Beetles

Charles Godfray and Michael Hassell

Ecologists have known since the pioneering work of May in the mid-1970s (*1*) that the population dynamics of animals and plants can be exceedingly complex. This complexity arises from two sources: The tangled web of interactions that constitute any natural community provide a myriad of different pathways for species to interact, both directly and indirectly. And even in isolated populations the nonlinear feedback processes present in all natural populations can result in complex dynamic behavior. Natural populations can show persistent oscillatory dynamics and chaos, the latter characterized by extreme sensitivity to initial conditions. If such chaotic dynamics were common in nature, then this would have important ramifications for the management and conservation of natural resources. On page 389 of this issue, Costantino *et al.* (*2*) provide the most convincing evidence to date of complex dynamics and chaos in a biological population—of the flour beetle, *Tribolium castaneum* (see figure).

It has proven extremely difficult to demonstrate complex dynamics in populations in the field. By its very nature, a chaotically fluctuating population will superficially resemble a stable or cyclic population buffeted by the normal random perturbations experienced by all species. Given a long enough time series, diagnostic tools from nonlinear mathematics can be used to identify the telltale signatures of chaos. In phase space, chaotic trajectories come to lie on "strange attractors," curious geometric objects with fractal structure and hence noninteger dimension. As they move over the surface of the attractor, sets of adjacent trajectories are pulled apart, then stretched and folded, so that it becomes impossible to predict exact population densities into the future. The strength of the mixing that gives rise to the extreme sensitivity to initial conditions can be measured mathematically estimating the Liapunov exponent, which is positive for chaotic dynamics and nonpositive otherwise. There have been many attempts to estimate attractor dimension and Liapunov exponents from time series data, and some candidate chaotic population have been identified (some insects, rodents, and most convincingly, human childhood diseases), but the statistical difficulties preclude any broad generalization (*3*).

Cannibalism and chaos. The flour beetle, *Tribolium castaneum*, exhibits chaotic population dynamics when the amount of cannibalism is altered in a mathematical model.

An alternative approach is to parameterize population models with data from natural populations and then compare their predictions with the dynamics in the field. This technique has been gaining popularity in recent years, helped by statistical advances in parameter estimation. Good ex-

---

The authors are in the Department of Biology, Imperial College at Silwood Park, Ascot, Berks, SL5 7PZ UK. E-mail: m.hassell@ic.ac.uk

amples include models of measles dynamics (*4*) and of boreal rodents (*5*). The drawback, of course, is that the predictions may be highly model-dependent, an outcome that is hard to identify if validation is purely through comparison with limited time series data obtained by observation. Ideally one would like to use the model to design manipulative experiments for the field, but this has so far proven elusive.

So, if not in the field, what about the laboratory? Population ecologists are often ambivalent about moving indoors, pejoratively referring to what Kareiva (*6*) has dubbed "bottle experiments" and to their use as analog computers. Yet many of the fundamental concepts underlying modern population ecology were formulated after studies of laboratory populations of blow flies (*7*), flour beetles (*8*), and ciliates (*9*) in the 1930s and 1940s. The work of Costantino *et al.* forcibly argues for the continuing value of bottle experiments.

They studied the flour beetle, *T. castaneum*, a classic laboratory model insect. *Tribolium* can be kept in milk bottles supplied with flour or bran; eggs are laid in the medium, the insect taking about 2 weeks to reach the pupal stage and a further fortnight to become a reproductive adult. *Tribolium* is cannibalistic: older larvae eat smaller larvae and adults consume larvae and pupae. Cannibalism is the main feedback mechanism limiting population growth.

In previous studies (*10*, *11*) the group had found that the dynamics of the system could be approximated by a straightforward model consisting of three coupled difference equations representing the change in densities of larvae, pupae, and adults over a 2-week period. Three nonlinear terms represented the effects of cannibalism. To parameterize the model, they converted the deterministic skeleton into a stochastic model through the addition of multivariate normal noise on a logarithmic scale. The parameters and noise variance-covariance matrix were then estimated with maximum-likelihood techniques.

The model predicts that the dynamics of the system depends critically on parameters such as the adult mortality rate and the fraction of pupae that mature into adults. In a previous study, Costantino *et al.* manipulated adult mortality. The model predicted that as mortality increased the beetle dynamics should move from stable equilibrium through cycles to a second region of stable equilibrium, to quasiperiodicity. Quasiperiodicity occurs when trajectories move over the surface of an attractor and never exactly repeat each other (think of a rotational transformation with an angle that is an irrational multiple of π). Quasiperiodicity is different from chaos, because it does not show extreme sensitivity to initial conditions (the Liapunov exponent is zero). However, in bifurcation studies, quasiperiodicity frequently presages chaos and is an alternative to the more familiar period doubling route to chaos. The results of the experiments provided impressive confirmation of the model predictions.

In the new study, Costantino *et al.* manipulate recruitment to the adult stage. As the severity of adult cannibalism of pupae increases, the system moves from stable equilibrium to quasiperiodicity, the aperiodic cycles becoming phase-locked to give regular cycles, followed by chaos. For even higher levels of cannibalism, regular cycles are again observed and there is also a region of multiple attractors. Again, the results of the experiments are impressively consistent with the model.

Without doubt, the experiments on *Tribolium* are the clearest experimental demonstration of quasiperiodicity and chaos. These results will encourage similar studies in other systems. Some problems remain, however. First, the identification of the complex dynamic behavior in the different time series is largely through inspection. We need better statistical techniques to allow more objective characterization. Second, the *Tribolium* system is extremely artificial and extrapolation to other systems difficult. Cannibalism is an extremely potent feedback mechanism, which predisposes the system to show complex dynamics. The absence of a spatial dimension, other species, or of biological evolution (all individuals were periodically replaced by the same number of beetles from stock cultures) may all have acted to make complex dynamics more (or less) likely. But these caveats aside, ecologists at last have a convincing example of chaos that they can use as a base to understand better complex dynamics in other laboratory systems and, more importantly, in the field.

References

1. R. M. May, *Science* **186**, 645 (1974).
2. R. F. Costantino, R. A. Desharnais, J. M. Cushing, B. Dennis, *ibid.* **275**, 389 (1997).
3. A. Hastings, C. L. Hom, S. Ellner, P. Turchin, H. C. J. Godfray, *Annu. Rev. Ecol. Syst.* **24**, 1 (1993).
4. B. M. Bolker and B. T. Grenfell, *Proc. R. Soc. London Ser. B* **251**, 75 (1993).
5. I. Hanski, P. Turchin, E. Korimaki, H. Henttonen, *Nature* **364**, 232 (1993).
6. P. M. Kareiva, *Perspectives in Ecological Theory*, J. Roughgarden, R. M. May, S. A. Levin, Eds. (Princeton Univ. Press, Princeton, 1989), p. 68.
7. A. J. Nicholson, *Aust. J. Zool.* **2**, 9 (1954).
8. T. Park, *Physiol. Zool.* **27**, 177 (1954).
9. G. F. Gause, *The Struggle for Existence* (Williams & Wilkins, Baltimore, 1935).
10. R. F. Costantino, J. M. Cushing, B. Dennis, R. A. Desharnais, *Nature* **375**, 227 (1995).
11. B. Dennis, R. A. Desharnais, J. M. Cushing, R. F. Costantino, *Ecol. Monogr.* **65**, 261 (1995).

NEUROSCIENCE

Synapse Elimination: For Nerves It's All or Nothing

Eric Frank

In muscles of adult vertebrates, each muscle fiber is innervated by a single motoneuron. This is not true at birth, however, when several motoneurons innervate each fiber. Then over the next 2 weeks, in a process called synapse elimination, motoneurons give up their connections with most of these muscle fibers so that each fiber is left with a single input. The experiments described by Colman *et al.* (*1*) on page 356 of this issue provide the first account of the physiological changes in synaptic transmission that occur during synapse elimination.

Colman *et al.* studied these changes by recording intracellularly from muscle fibers, while separately stimulating two motoneurons that innervated a single site on the fiber. They determined the strength of each input by measuring the number of quantal packets of the neurotransmitter acetycholine (ACh) each motoneuron released. The change from multiple to single inputs occurs progressively rather than suddenly. Shortly after birth, when most muscle fibers are still multiply innervated, the inputs usually differ in strength by less than a factor of 2, as indicated in panel A of the figure. After a week, however, the strength of the two inputs diverges, with one-third of the remaining multiply-innervated fibers having inputs that differ by more than fourfold. The subsequent panels of the figure illustrate this process: the input from axon 2 becomes progressively stronger (indicated by the increase in the

---

The author is in the Department of Neurobiology, University of Pittsburgh, Pittsburgh, PA 15261, USA. E-mail: efrank+@pitt.edu