

Ecology

# Nonlinearity and the Moran effect

The study of synchronization phenomena in ecology is important because it helps to explain interactions between population dynamics and extrinsic environmental variation<sup>1–5</sup>. Grenfell *et al.*<sup>1</sup> have examined synchronized fluctuations in the sizes of two populations of feral sheep which, although situated on close but isolated islands, were nevertheless strongly correlated (observed value of the population correlation,  $r_p$ , 0.685). Using a nonlinear threshold model, they argue that this level of population correlation could only be explained if environmental stochasticity was correlated between the islands, with the environmental correlation,  $r_e$ , higher than 0.9 “on average” (Fig. 1a). This unusually high environmental correlation is far greater than would be predicted by the Moran effect<sup>2</sup>, which states that the population correlation will equal the environmental correlation in a linear system. Grenfell *et al.*<sup>1</sup> imply that a simple nonlinearity in population growth can mask or even destroy the Moran effect<sup>1,3,4</sup>. Here we show that these surprising results are an artefact of the techniques used to measure noise correlations and synchronization.

In their simulations<sup>1</sup>, Grenfell *et al.* based all correlation calculations on a time series of  $n=800$  model samples, which is far larger than the  $n=18$  pairs of observed sheep-population data. To obtain a correct comparison of the model with their observed results, we repeated their calculations, but examined only  $n=18$  pairs of simulated data samples for each model run; these smaller sample sizes should tend to increase statistical variability in the analysis.

Our study of an ensemble of simulation runs revealed that only a very weak environmental correlation  $r_e$  (calculated as for Fig. 1b) is required for the model populations frequently to achieve a correlation  $r_p$  greater than or equal to the observed correlation  $r=0.685$ . As Fig. 1d reveals, the observed correlation (or higher) can be found by chance alone, appearing in about one in 20 simulations for  $r_e=0.3$ , and then much more frequently as  $r_e$  increases.

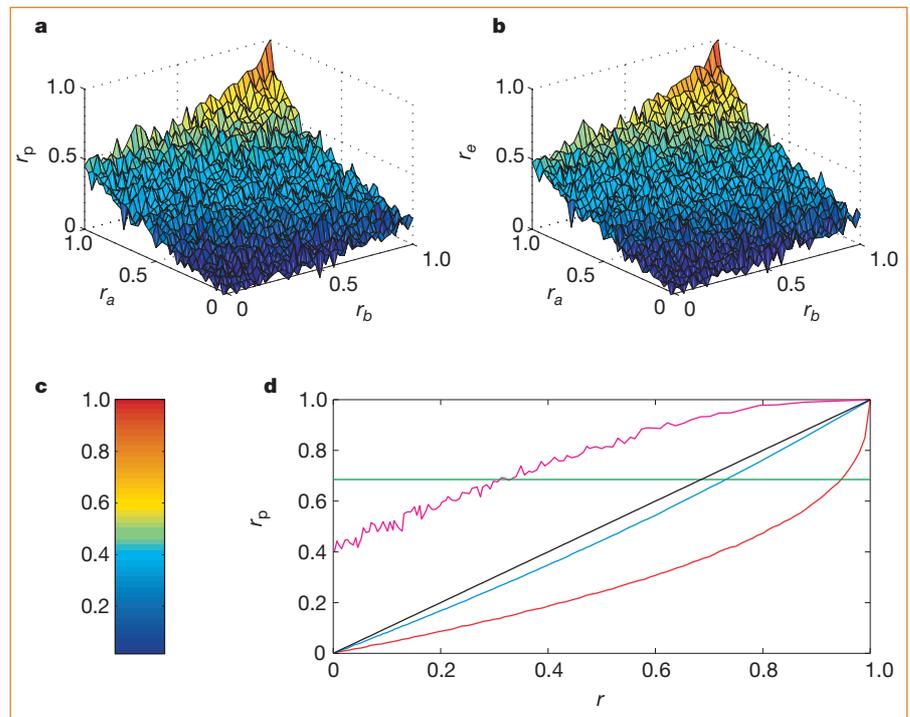
The main conclusion of Grenfell *et al.*, that very strong environmental correlation ( $r_e > 0.9$ ) is responsible for the observed synchronized sheep-population fluctuations, therefore needs further consideration if a far smaller environmental correlation ( $r_e = 0.3$ ) can equally well explain the same dynamics. By failing to take into account the lengths of the ecological time series, their analysis may have misinterpreted the causes of synchrony in these feral sheep populations.

The Moran effect predicts that a plot of population correlation versus environmental correlation will yield a straight line of unit slope if the two synchronized systems are linear. By measuring  $r_e$  in the manner intended by Moran<sup>2</sup> (Fig. 1b, legend), we find that the nonlinear threshold model<sup>1</sup> provides results that scale very closely to the linear relationship (Fig. 1d), so the Moran effect survives. When  $r_p$  and  $r_e$  are plotted over the entire range of parameters used in ref. 1 (Fig. 1a and b, respectively), the two graphs are almost identical and  $r_e \approx r_p$ , a clear demonstration of the Moran effect.

Why then did Grenfell *et al.* fail to reproduce the Moran effect? In their approach, the environmental correlation  $r_e$ , as set by their model's control parameters, is often unrepresentative, as shown by the following argument. The environmental shocks actually experienced by the sheep populations

have, by construction, correlation  $r$  only when the populations are both above or below a fixed threshold level; but when one population is above threshold and the other below, a situation that can sometimes constitute half of any simulation run, the respective environmental shocks at the two islands are, again by construction, uncorrelated. These long periods of decorrelation can cause the true environmental correlation,  $r_e$ , calculated over the entire simulation run, to be markedly less than the value  $r$  defined by the model parameters. It is due to this misestimation of correlation (and not because of the presence of a nonlinear threshold<sup>1,3,4</sup>) that Grenfell *et al.*<sup>1</sup> require an unusually high environmental correlation to yield the observed sheep synchrony.

Grenfell *et al.* have demonstrated the potential of using nonlinear statistical models for ecological investigations.



**Figure 1** Simulation results using the nonlinear threshold model with density-dependent switching between two independent environmental noise components, as described by Grenfell *et al.*<sup>1</sup>. **a**, Correlation between island sheep populations,  $r_p$ , as a function of the model's noise parameters  $r_a$  and  $r_b$  (Fig. 3a of ref. 1). The model<sup>1</sup> is set up so that  $r_a$  and  $r_b$  represent the correlation of the environmental noise affecting the two sheep populations when they are both either above or below threshold, respectively (see **c** for colour calibration). According to ref. 1,  $r_p$  equals the observed value of  $r_o = 0.658$  only if the environmental correlations  $r_a$  and  $r_b$  are larger than “0.9 on average”. **b**, True environmental correlation,  $r_e$ , as a function of the model parameters  $r_a$  and  $r_b$ . To calculate  $r_e$ , we stored all environmental shocks received by each model sheep population and then simply determined their correlation: hence  $r_e$  is viewed as the correlation coefficient of shocks directly experienced by the two model sheep populations. The surface for  $r_e$  is almost identical to that of  $r_p$  in **a**, demonstrating a Moran effect. **c**, Colour-coding of correlations depicted in **a** and **b**. **d**, Analysis of systems in which model environmental correlation parameters  $r = r_a = r_b$  (that is, systems along the diagonal of parameter space in **a** and **b**). Red curve, cut through surface in **a** above the line  $r = r_a = r_b$ . The correlation between sheep populations  $r_p$  is plotted against the model's environmental correlation parameter  $r$ ; the deviation from the reference diagonal (black) seems to indicate the absence of a Moran effect, as argued in ref. 1. Blue curve,  $r_p$  vs  $r_e$ , where  $r_e$  (horizontal axis) is the true environmental correlation (see **b**). Note that this line is very close to the reference diagonal (black), where  $r_p = r_e$ , as predicted by the Moran effect. Magenta line, effects of small sample size ( $n=18$ ) due to statistical scattering in an ensemble of 1,000 simulation runs: for each value of environmental correlation  $r_e$  (horizontal axis), 5% of the simulations have  $r_p$  values larger than the value plotted. Green horizontal line, the measured correlation between the two observed sheep populations is  $r_o = 0.685$ . The point of intersection of the green and magenta lines yields the minimum value of the ‘true environmental correlation’,  $r_e$ , for which we can expect to find the observed sheep correlation by chance alone (that is, in at least 1 in 20 runs, or 5%, when  $r_e = 0.3$ ). Further details are available from the authors.

Refining these techniques should increase our understanding of the relation between environmental fluctuations and population dynamics, in the spirit of Moran.

**Bernd Blasius, Lewi Stone**

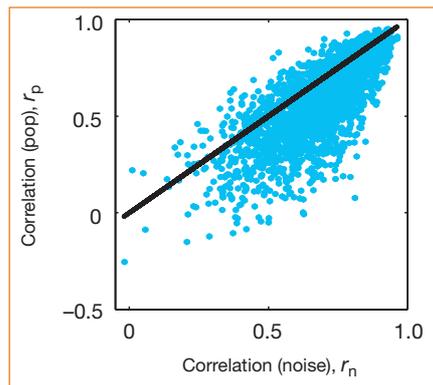
*The Porter Super-Center for Ecological and Environmental Studies,  
Department of Zoology, Tel Aviv University,  
Ramat Aviv, Tel Aviv 69978, Israel  
e-mail: lewi@lanina.tau.ac.il*

1. Grenfell, B. T. *et al. Nature* **394**, 674–677 (1998).
2. Moran, P. A. P. *Aust. J. Zool.* **1**, 291–298 (1953).
3. Stenseth, N. C. & Chan, K.-S. *Nature* **394**, 620–621 (1998).
4. Hudson, P. J. & Cattadori, I. M. *Trends Ecol. Evol.* **14**, 1–2 (1999).
5. Blasius, B. *et al. Nature* **399**, 354–359 (1999).

*Grenfell et al. reply* — The Moran effect refers to systems of population dynamics that are linear: under these circumstances, the long-term correlation between population densities will be the same as the correlation between the random environmental perturbations. The Soay sheep exhibit significant nonlinearity in their density dependence (Fig. 2a of ref. 1). At low populations, numbers tend to increase exponentially, with mean growth rate  $r=0.24$ , whereas at high densities (above a threshold of 1,172 animals), the population tends to decline, with mean  $r=-0.29$ . Thus, when populations on two adjacent islands are both above their thresholds, both will tend to decline, and when both are below their thresholds, both will tend to increase.

This immediately introduces a positive correlation between population dynamics on adjacent islands in the absence of any environmental forcing. When one population is above the threshold and one is below, the expectation is of no short-term correlation because the trends will tend to cancel out. Adding noise to the system has two effects. Correlated noise tends to push the dynamics into synchrony, because both populations tend to crash to low densities during the same years (for example, those with the most extreme winter weather). The nonlinearity means, however, that the same stochastic event could drive one population below the threshold but leave another population above it (for example, if initial population densities are sufficiently different). In this case, the two populations would experience different regimes of density dependence during the same year and synchrony would be reduced. Intuitively, then, in the presence of nonlinear density dependence, environmental forcing has to be stronger if it is to drive the populations into synchrony and keep them there.

Blasius and Stone have pointed out two problems with our analysis. First, they show that we had the two populations experiencing different — hence uncorrelated — noise during periods when the two populations were on opposite sides of the threshold. Correcting this mistake reduces the level



**Figure 1** Scatter plot (blue) of inter-island population correlation ( $r_p$ ) against true noise correlation ( $r_n$ ) for 3,000 simulations (each of 18 time points) of the SETAR model, defined as in Table 1 of ref. 1, with the correction in noise realization proposed by Blasius and Stone. The black line indicates where population correlation equals the noise correlation (the expectation of the Moran effect). See ref. 2 for more details.

of noise correlation ( $r_n$ ) required to produce the observed level of population correlation ( $r_p$ ) ( $r_p=0.685$ ) from  $r_n>0.9$  to around 0.8 for large samples. This means that the extra-Moran effect is reduced, but not abolished.

Their second point is that, with realistically short time series (such as our 18 points), variability in the inter-population correlation coefficient generates a relatively high expectation of observing correlations higher than Moran, leading to inflated type-I errors. We have carried out further calculations with the corrected model that agree qualitatively with this. However, even short model simulations show the imprint of nonlinearity in their aggregate correlation structure — a strong downward bias in population correlation for a given level of noise correlation, compared to various linear null models (Fig. 1; for more details, see ref. 2). Thus, the impact of nonlinearity on population correlation is apparent in the collective behaviour of short simulations, as well as in individual realizations of the model's long-term dynamics.

There are several important directions for studies on the interactions between noise and determinism in population dynamics. Most important is an increase in the realism of the underlying model. The inclusion of age- and sex-structure effects is essential, because we know that animals of different ages and sexes experience markedly different patterns of mortality<sup>3</sup>. A further improvement would incorporate threshold density as a random variable rather than a constant (it is intraspecific competition for food that underlies the density dependence, and food supply determines the sheep density at which competition kicks in). This would allow for island-to-island differences in the response of food availability to environmental noise, so that islands with the same population densities could experience

different density-dependence regimes in the same year.

The ability to detect extra-Moran correlations depends critically on the balance between noise and density dependence (B. Blasius and L. Stone, personal communication), so any model refinement that explains more variability in terms of population processes will increase our powers of evaluation. Technically, developments in nonlinear time-series analysis need to encompass estimation of age<sup>4</sup> and spatial heterogeneities, as well as the dissection of process noise from measurement error. This is particularly important for the relatively short time series found in ecology, where even linear time-series models can produce a complex range of correlation behaviours<sup>2</sup>.

A thorough understanding of spatial dynamics can only come about once the interaction between correlated noise and nonlinear density dependence is understood through long-term ecological studies, combined with models.

**B. T. Grenfell\***, **B. F. Finkenstädt†**,

**K. Wilson‡**, **T. N. Coulson§**, **M. J. Crawley||**

\**Zoology Department, University of Cambridge,  
Downing Street, Cambridge CB2 3EJ, UK*

†*Department of Statistics, University of Warwick,  
Coventry CV4 7AL, UK*

‡*Institute of Biological Sciences, University of  
Stirling, Stirling FK9 4LA, UK*

§*Institute of Zoology, Zoological Society of London,  
Regent's Park, London NW1 4RY, UK*

||*Imperial College, Silwood Park, Ascot SL5 7PY, UK*

1. Grenfell, B. T. *et al. Nature* **394**, 674–677 (1998).
2. [www.zoo.cam.ac.uk/zoostaff/matt/GROUP/Download/](http://www.zoo.cam.ac.uk/zoostaff/matt/GROUP/Download/)
3. Grenfell, B. T., Price, O. F., Albon, S. D. & Clutton-Brock, T. H. *Nature* **355**, 823–826 (1992).
4. Leirs, H. *et al. Nature* **389**, 176–180 (1997).

Physiology

## An actively controlled heart valve

Vertebrate hearts typically have cardiac valves that are thin and leaf-like and which work passively, allowing blood to move forward during systole and preventing it from flowing back during diastole. Crocodilian hearts have nodules of connective tissue, resembling opposing knuckles, or cog-teeth<sup>1–3</sup>, in the subpulmonary conus just proximal to the pulmonary valves. Here we show that these cog-teeth act in the estuarine crocodile *Crocodylus porosus* (Fig. 1) as a valve that regulates the flow of blood between the lungs and the systemic circulation in response to a  $\beta$ -adrenergic mechanism. To our knowledge, this is the first report of an actively controlled intra-cardiac valve in a vertebrate.

Among the vertebrates, only the mammals, birds and crocodilians have anatomi-