

## Sources, sinks and chaos

In an recent issue of *TREE*, Dias<sup>1</sup> reviews the importance and complexity of source-sink habitats in ecology. She points out the difficulties of identifying the source-sink populations from a simple comparison of the demographic parameters between populations in a single generation study, and affirms that these situations can be correctly identified only by long-term demographic studies.

I think the above affirmation is true only for populations with a single stable-equilibrium density. The difficulty may persist for long-term demographic studies if the source population present chaotic behaviour<sup>2</sup>. For instance, using the source-sink model presented by Watkinson and Sutherland<sup>3</sup> with a source population with chaotic dynamic ( $\lambda = 100$ ,  $a = 0.01$  and  $b = 10$ ) and a sink population ( $\lambda = 0.8$ ,  $a = 0.01$  and  $b = 1$ ) with migration rates of, say,  $m_1 = 0.6$  and  $m_2 = 0.1$ . We can calculate the net rate of population increase ( $R$ ), which is a measure of the number of births and deaths that occur, in order to identify source and sink populations ( $R < 1$  corresponds to sink populations). After a simulation of 100 generations to see the long-time population behaviour, the last three outcomes for the chaotic population are:

Generation	$R$
98	0.15
99	58.1
100	0.02

We can see that sometimes the population behaves as a source (e.g.  $R = 58.1$ ) and sometimes as a sink (e.g.  $R = 0.15$ ) owing to the chaotic behaviour of the population, showing the difficulties of discerning between source and sink populations even in long-term studies.

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### References

- 1 Dias, P.C. (1996) *Trends Ecol. Evol.* 11, 326-330
- 2 Hastings, A. et al. (1993) *Annu. Rev. Ecol. Syst.* 24, 1-33
- 3 Watkinson, A.R. and Sutherland, W.J. (1995) *J. Anim. Ecol.* 64, 126-130

## Reply from P.C. Dias

I agree with González-Andujar that it may be difficult to identify clearly source and sink populations even from long-term demographic studies. It is also true that ecological thinking has been dominated by equilibrium concepts<sup>1</sup>, and that other kinds of population dynamics, such as stochastic or chaotic behaviour, should not be ignored. However, I would like to reiterate a few points concerning the source-sink model as defined by Pulliam<sup>2</sup>.

First, Pulliam has defined source and sink populations in terms of 'BIDE' models, that is, models that include not only birth and death rates, but also emigration and immigration rates. Birth and death are insufficient to identify sources and sinks, whatever the length of the study (cf. Ref. 3). Second, his definitions<sup>2</sup> of source and sink apply 'to equilibrium populations only', and thus are not suited for chaotic populations. Third, his model<sup>2</sup> implies active dispersal (i.e. habitat selection based on differences in habitat quality), and I am not aware of population models that include both chaotic behaviour and habitat choice. I therefore believe that restrictions concerning chaotic behaviour are not relevant in a genuine source-sink context: such a behaviour would question the definition of a 'source' population rather than its identification.

Identifying source and sink populations from a model mainly implies knowing population sizes at each generation. But in the real world, source-sink functioning is a biological concept that includes other demographic parameters as well as other factors like habitat heterogeneity, density dependence or individual behaviour (e.g. habitat selection).

Anyway, definitions of sources and sinks are conceptual tools, not rigid labels, so they may not always strictly fit natural populations. It is healthy to keep in mind that nature is not generated by models.

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## Social terminology: what are words worth?

Debating Costa and Fitzgerald<sup>1</sup> over the merits of using within group distribution of reproduction as the key criterion for understanding 'eusociality', Reeve et al.<sup>2</sup> criticized 'the idea (attributed to Wcislo [sic]) that it is best not to categorize societies at all, but rather simply to note and describe each taxon as a phylogenetically unique entity.' This misrepresents my views<sup>4</sup>, and misses two important points.

The first point relates to the function of definitions of terms like 'eusociality'. Costa and Fitzgerald<sup>3</sup> (p. 288) carefully quoted from Wcislo<sup>4</sup> that authors should state 'precisely and explicitly how they operationally define...[social behaviors]...for the specific hypotheses they wish to test.' Definitions are conceptual tools, and different questions require different frameworks<sup>5</sup>. For example, if one wanted to test the hypothesis that groups are more efficacious than solitary individuals in defending nests against predators, then appropriate categories are 'group-living' or

'solitary', rather than ones derived from within-group distribution of reproduction.

The second point relates to the use of phylogenetic data in evolutionary studies. Reeve et al. express concern that using a 'phylogenetically unique entity' as a basis for comparison will 'block the fundamental scientific goal...of seeking common causal principles underlying convergent phenomena.' This concern is puzzling since phylogenetic information is required to distinguish between convergent and homologous traits. Comparing phylogenetically distant species like birds and bees, as well as closely related species, can give valuable insights regarding general patterns of evolution, and the two kinds of comparisons serve different ends.

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- 2 Reeve, H.K., Sherman, P.W. and Keller, L. (1996) *Trends Ecol. Evol.* 11, 472
- 3 Costa, J.T. and Fitzgerald, T.D. (1996) *Trends Ecol. Evol.* 11, 285-289
- 4 Wcislo, W.T. in *Evolution of Social Behavior in Insects and Arachnids*, Cambridge University Press (in press)
- 5 Lee, P.C. (1994) in *Behavior and Evolution* (Slater, P.J.B. and Halliday, T.R., eds), pp. 266-303, Cambridge University Press

## Sewall Wright meets artificial life

It was a real pleasure to see Toquenaga and Wade's article on why A- and B-life research have failed to interact as much as at least some researchers in both fields were (and still are) hoping<sup>1</sup>. I would simply like to highlight a couple of points for further discussion.

First, the authors point out that the type of mutational effects influencing A- and B-life systems are different, with mostly mutations of minor effect being typical of real organisms, and mutations of large effect being more characteristic of A-life. However, this is more a conventional assumption than it is a fact, at least when it comes to the genetic basis of phenotypic novelties. While it is true that many mutations in living organisms are neutral or quasi-so when they occur, several authors have recently pointed out that the *evolutionary role* of a reduced number of loci with major effects on the phenotype might have been underestimated owing to the influence of the fisherman paradigm<sup>2,3</sup>.

Second, one of the reasons that there has been little enthusiasm in the B-life community about A-life accomplishments is because several A-life researchers have simply rediscovered (and sometimes renamed without acknowledging, or knowing about) fundamental theorems of population and quantitative genetics. One can get