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Simple laboratory tests of ecological theories: what we can learn from them, and when we should be cautious

Population ecology is concerned with understanding the mechanisms behind the maintenance of, and fluctuations in, natural population sizes. Behavioural and physiological differences among individuals lead to differences in birth and survival rates within and between populations, while dispersal of individuals links populations that are spatially separated. Such a collection of interacting populations of the same species is called a metapopulation. Various mathematical functions have been developed that try to capture the most crucial aspects of population growth and regulation in a simple framework (e.g. Verhulst 1838; Volterra 1926; Lotka 1932; Ricker 1954; Maynard-Smith and Slatkin 1973; Hassell 1975). Functions of this form, particularly those that focus on populations that reproduce in discrete time steps, are known to exhibit a rich variety of dynamical behaviours, from stable equilibrium dynamics to two point cycles through more complex dynamics including chaotic fluctuations (May and Oster 1976). Introducing a spatial element into these models can have varying results, sensitive to the specific underlying assumptions (see Bowler and Benton 2005 for a recent review). Models such as these form the backbone of theoretical population ecology.

There is a long history of testing theories of population ecology. Valuable work has been carried out in controlled laboratory (microcosm) settings (e.g. Gause 1932; Huffaker 1958), while more recently attempts have been made to carry out large scale field experiments (Krebs *et al* 1995; Korpimäki *et al* 2003). Time-series analysis of population fluctuations may also allow us to understand what drives characteristic fluctuations in population sizes over time and how these fluctuations can be synchronized over spatially separated populations (Ranta *et al* 1995; Lindström *et al* 1996; Hudson and Cattadori 1999; Cattadori *et al* 2000). The question of large scale synchrony in population fluctuations remains another intriguing area of population ecology research (Bjørnstad *et al* 1999; Ranta *et al* 2006).

Previously, the ability of models to explain fluctuations in laboratory populations has been examined by fitting existing population data to the different model functions to assess which model fit the data best (e.g. Bellows 1981). This method has an obvious drawback as the underlying assumptions of the models were not always met by the experiments that generated the data. Over the last decade or so, serious attempts have been made to examine how different types of population dynamics can arise in carefully controlled laboratory populations (Constantino *et al* 1995; Bjørnstad *et al* 1998; Mueller and Joshi 2000; Dennis *et al* 2001; Benton and Beckerman 2005). A recent article by Dey and Joshi (2006) is an interesting contribution to this field, as it explicitly uses a method of dispersal that is often used in simple mathematical models of spatially structured populations. While metapopulation studies are traditionally concerned with extinction and recolonization processes that are considered at the ensemble level (Hanski 1999), Dey and Joshi (2006) consider sub as well as metapopulation level processes. In their simple laboratory design, they allowed *Drosophila melanogaster* individuals to interact and reproduce in vials, with each vial so positioned that the whole formed a ring of spatially distinct populations. Dispersal of adults between vials occurred 21 days after they were laid as eggs. Dey and Joshi (2006) tested three different dispersal rates between each population and its two immediately neighbouring populations (0, 10% and 30%) by transferring the appropriate number of individuals between the corresponding vials, to determine whether this led to any differences in population fluctuations at the local and ensemble (metapopulation) levels. Nearest neighbour dispersal has been commonly incorporated into a large number of both analytical and simulation studies of population growth, and this experimental test is a worthwhile examination of the effects in a laboratory population. The authors showed that there were differences in the magnitude of subpopulation fluctuations as well as the degree of synchrony between populations under the different dispersal treatments. Fluctuations in subpopulations with a 10% dispersal rate were higher than those with 30% dispersal rate. Population sizes between neighbouring patches showed signs of asynchrony under the 10% treatment, with more synchronized fluctuations under the 30% treatment.

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Another feature of the results is a phenomenon known as the 'portfolio' effect. The origins of the portfolio effect go back all the way to Daniel Bernoulli's critique of probability theory (Stearns 2000). Its more modern roots lie in studies of stock market fluctuations, where a bet-hedging strategy means that having a diversity of stock types will spread the risk, as a decrease in the value of some stocks will be balanced out by increases in other types of stocks. Dey and Joshi's (2006) results show that fluctuations measured at the level of the individual patch (i.e within each vial) appear relatively higher than those seen at the metapopulation level; although no explicit statistical comparison has been provided, this would undoubtedly be of interest. The portfolio effect is also known in ecology from biodiversity studies, where fluctuations in community biomass are less than those experienced by individual species or functional groups (Ives *et al* 1999). A comparison of the local extinction rates in the different dispersal treatments would also be important and interesting in terms of metapopulation studies, but such a comparison has not been presented by Dey and Joshi (2006).

An unfortunate drawback of this experimental design is the high extinction rate in the zero-dispersal (control) treatment, coupled with the re-introduction of eight individuals (four males, four females) following each local extinction in the control. No individuals were added to the other dispersal treatments following local extinctions – nearest neighbour dispersal was sufficient to rescue extinct populations. Therefore it is not reasonable to compare the results from the control to the other treatments. A simple way to resolve this may have been to have a second control treatment for each positive dispersal rate, to which eight individuals were added along with the nearest neighbour dispersers whenever a local extinction event occurred. However, the comparison of the 10% and 30% dispersal rates remains interesting, as these results confirm previous theoretical predictions about the expected increase in synchrony between subpopulations with increasing dispersal rates. A surprising aspect of the results is the fact that low (10%) dispersal rates showed asynchronous fluctuations between neighbouring patches. This is contrary to theoretical predictions, where even small amounts of dispersal are expected to lead to an increase in synchrony compared to populations with no dispersal. Full interpretation of these experimental results remains difficult, due to the lack of a proper control.

Similarities between experimental and simulation results should be evaluated with caution. Here we point out some of the most important factors worth considering. First, it is not always straightforward to decide which of the many alternative theoretical models is most appropriate to describe your experimental system. In the worst case there may be many alternative models that fit the data equally well (or poorly), where model selection becomes rather subjective. It is good practice to compare several candidate models before making a final decision (e.g. Sheeba and Joshi 1998). Dey and Joshi (2006) used the Ricker (exponential logistic) function $\{N_{t+1} = N_t \exp[r(1 - N_t / K)]\}$ based on previous experience of a similar experimental system (Sheeba and Joshi 1998). It becomes crucial to consider the underlying assumptions of the model at this point. Superficial similarities between experimental and simulation data could mask the fact that dynamical similarities are produced by different underlying mechanisms. Here, the biology of *D. melanogaster* should be compared to the model assumptions. Once a suitable model has been selected, model parameters are estimated. The error associated with the estimation of each parameter increases as the number of parameters in the model increases. In their chapter on *Drosophila*, Mueller and Joshi (2000) discuss a large body of work from *D. melanogaster* population studies, and show the importance of understanding the outcome of competitive effects between individuals at different life-history stages. Although they have shown that the unstructured Ricker function can capture many of the dynamical characteristics of *D. melanogaster* populations, there is a concern that the mechanisms that lead to this dynamical similarity differ between the real *Drosophila* populations and the model function used in the simulations. Readers should be aware of this when they interpret the results of the study by Dey and Joshi (2006).

In summary, the work by Dey and Joshi (2006) supports the assertion that an excellent way to test simple ecological theories is by using simple laboratory experiments. They go on to illustrate their points in combination with the results of a simple simulation experiment. However, we must interpret the overall results and conclusions cautiously, remembering that it is crucial to ensure that the underlying assumptions of both the theory and the experimental design match. Population ecology is maturing as a research discipline, and the distance between theoretical and empirical work is shrinking all the time. With their uncomplicated, yet elegant experimental approach, Dey and Joshi (2006) have demonstrated one way to bridge the gap by empirically testing commonly used theoretical approaches.

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MIKE S FOWLER*
LASSE RUOKOLAINEN
Integrative Ecology Unit,
Department of Biological and Environmental Sciences
PO Box 65, Viikinkaari 1,
FI-00014 Helsinki University Finland
*(Email, mike.fowler@helsinki.fi)