

## Ecology

## Predicting fruitfly guild sizes

from John H. Lawton

ONE aim of theoretical ecology is to predict the number of species able jointly to exploit a common resource in a similar fashion, that is to predict guild sizes<sup>1</sup>. Traditionally, the problem has been approached by partitioning the requirements of each species within the guild along some 'resource-axis'. By determining the total supply of resources, and each species' requirements and overlapping demands, the number of species able to coexist can be predicted<sup>2,3</sup>, at least in theory. This yields some interesting insights, but the difficulties of estimating the intensity of competition between species makes quantitative predictions about real guilds appear hopelessly difficult, not least because of the snowstorm of parameters required (for example, ref. 4). But new work<sup>5,6</sup> appears to be much more successful in predicting the number of species that can coexist within a guild.

One alternative approach retains the emphasis on interspecific competition, expressed by the competition coefficients of the Lotka–Volterra equations<sup>2,3</sup>, but avoids the complexities of the field by use of controlled experiments in the laboratory. Fruitflies (*Drosophila*) are suitable animals to work with because large numbers of different species can be kept in pure cultures and guilds of various sizes can be assembled by pooling populations of any number of species. This approach is the one adopted by Michael Gilpin and his co-workers in California<sup>6</sup> over the past 10 years. The results are interesting in many

ways, but in the present context are actually rather simple. Starting with mixtures of 10 different species, over a range of initial densities, the cultures always collapsed to a maximum of no more than three species (7 out of 30 trials), and usually less (two coexisting species in 21 trials, and a single victor in one other).

Intriguingly, real *Drosophila* guilds in the field are conspicuously larger than this. The 'field' in this case consists of a variety of small, patchily distributed, ephemeral breeding sites used by *Drosophila*, ranging from rotting fruits and sap flows to fungal fruiting bodies and various flowers. In samples of 53 such sites from tropical and temperate habitats all over the world, Bryan Shorrocks and Jonathan Rosewell<sup>6</sup> find a modal guild-size of seven species. The reason why real *Drosophila* guilds are generally at least two or three times the size of laboratory guilds carries an important message for community ecology.

Gilpin's laboratory experiments deliberately exclude spatial heterogeneity because its inclusion would seem likely to make both experiments and models more difficult to construct and interpret. But paradoxically, as Shorrocks and Rosewell show<sup>6</sup>, incorporating spatial heterogeneity actually makes it easier and simpler to predict guild sizes, at least for *Drosophila*. Their approach also shifts emphasis away from competition coefficients as the key to understanding guild sizes, to the spatial distribution of species across resources.

For community ecology this is a dramatic change of emphasis. As Shorrocks and his colleagues show<sup>7</sup>, the spatial distribution of individual *Drosophila* species across breeding sites is highly clumped, a pattern that can be described simply, albeit somewhat crudely, by the negative binomial distribution.

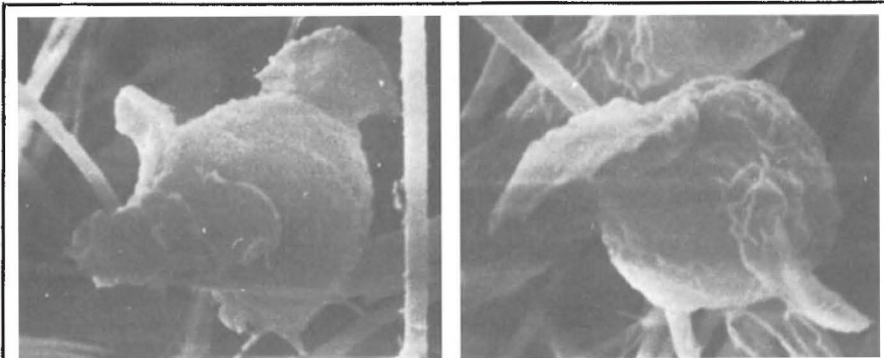
As long as different species of *Drosophila* have different, independent but sufficiently aggregated distributions, it is possible for more than two or three species to coexist quite happily in one type of breeding site. Even more interesting, a model of the interactions between several species in a spatially patchy world, incorporating sensible parameter values derived from real *Drosophila* populations, predicts a modal guild size of five or six species, encouragingly close to the observed number of seven. The frequency distributions of observed and predicted guild sizes are also reasonably similar, ranging from two species to about twenty.

The model is simple and works by allowing species to 'invade' the community sequentially, in order of their competitive dominance. Breeding sites left unused because of the clumped distribution(s) of the superior competitor(s), are then invaded by inferior species, until further invasion is no longer possible. However, the spatial refuges so created are not analogous to resource partitioning in more traditional models of community ecology, because each species redistributes itself after each generation, and distributions are not related to particular habitat variables or resource-axes such as moisture or degree of rotting. Nor is the outcome crucially dependent on the magnitude of the competition coefficients; more important is the degree to which species aggregate in their use of breeding sites.

This is very different from the previous ways in which ecologists have tried to understand how guild sizes are determined, and much more successful. It remains to be seen whether this kind of model will be useful for predicting guild sizes in other types of animals, and whether the match between observed and predicted guild sizes in *Drosophila* is roughly right for completely the wrong reasons. My own guess is that it is too good to be coincidence. □

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THE lineage fidelity of interleukin-3-dependent cells has for some time been the cause of uncertainty. In a recent private discussion, these cells were described as 'pigs to work with' and elsewhere I heard the view expressed that varied behaviours of these cells are 'somewhat horny'. While investigating the morphology of certain interleukin-3-dependent cell lines (left: AC2, 4,050 $\times$ ; right: 123, 2,550 $\times$ ), I can confirm that porcine and ovine attributes are indeed displayed by such cultures, as shown in the figure. In addition, there is a small but significant representation of whales, dolphins or tuna within the populations (data not shown), from which I conclude that interleukin-3-dependent cells may be somewhat fishy, and may perhaps need a pinch of salt in certain circumstances.

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