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Forum

Modularity, reproductive thresholds and plant population dynamics

Rees & Crawley (1989) suggest that, because of their modular construction, plants are less likely than unitary animals to display a size threshold for reproduction, and that they consequently have populations that are less prone to density-driven cycles or chaos. Their argument is based upon population models which show that the existence of a threshold rate of resource use below which individuals' fitness falls to zero is destabilizing (Beddington *et al.*, 1976; Lomnicki, 1988; Readshaw & Cuff, 1980).

To test their hypothesis Rees & Crawley examined the value of the *y*-intercept on curves of fitness (usually using fecundity as a surrogate) *vs* resource use (usually using size as a surrogate) for 35 animals and 15 plants. The exponents of log-log regressions of fecundity on plant weight were used for a further 11 plant species on the assumption that regressions with an exponent significantly greater than unity had a reproductive threshold. Apparently none of the 11 species met this criterion. The animals in this sample are unitary and the plants modular but the two groups also differ in many other ways that could influence the comparison, perhaps the most important of all being that the animals are heterotrophic and the plants autotrophic (see below). Whatever the result, the comparison is not a conclusive test of the influence of *modularity per se* on population dynamics.

Six of the 26 plant species in Rees & Crawley's sample had negative intercepts compared to 30 of the 35 animals. Rees & Crawley interpret this as unequivocal evidence that animals exhibit reproductive thresholds and that plants do not. However there are a number of grounds on which this conclusion can be questioned. Firstly, of the six plants with negative intercepts, three were statistically significant but of the 30 animals only seven were. Second, and more importantly, a size threshold for reproduction may exist without there being a negative intercept. Rees & Crawley make this point themselves, though they appear not to have appreciated that it invalidates their test. Virtually every semelparous perennial plant that has been studied has a size threshold for reproduction, including four (*Cynoglossum officinale, Cirsium vulgare, Dipsacus sylvestris, Oenothera glazioviana*) that appear in Rees & Crawley's sample as cases *without* a significant negative intercept. Since these plants have a minimum size for reproduction the *y*-intercept of their fitness/size regressions is a meaningless extrapolation because the *actual* curve of fitness *vs* size is non-linear. Non-linear relationships between size and reproductive efforts in plants were found to be quite common in a review by Samson & Werk (1986), all of whose data Rees & Crawley ignored.

Most perennial plants (and probably most animals) must reach a minimum size before they reproduce. A threshold in itself is not a sufficient condition for population instability. Instability results when the recruitment curve has a hump, and the diagonal line $N_t = N_{t+1}$ intersects the curve to the right of its maximum (e.g. Fig. 1a) (Vandermeer, 1981). Whether a threshold will be destabilizing or not depends upon how it affects the division of resources between reproductive and non-reproductive members of the population at high density (Lomnicki, 1988). If non-reproductives continue to consume resources when these are limiting, the recruitment curve may become humped and populations reaching the appropriate region of the curve will exhibit limit cycles or chaos. An actual case of this mechanism driving cycles in a plant population has been clearly documented for *Erophila verna* by Symonides, Silvertown & Andreasen (1986). At high density the proportion of the *E. verna* population flowering fell. Non-reproductives did not actually die, but continued to crowd reproductives, so that the latter were unable to consume extra resources (space) and produce extra seeds to compensate for the 'lost' seed production of the former, as would have occurred if non-reproductives had died (see below).

In general, the recruitment curve for an annual with no seed dormancy and 100% seed germination can be described by the difference equation (Watkinson, 1980):

$$N_{t+1} = \frac{\lambda N_t}{(1 + aN)^b} \qquad \text{Equation 1}$$

Where λ is the maximum possible value of the finite rate of increase, and a and b are constants.

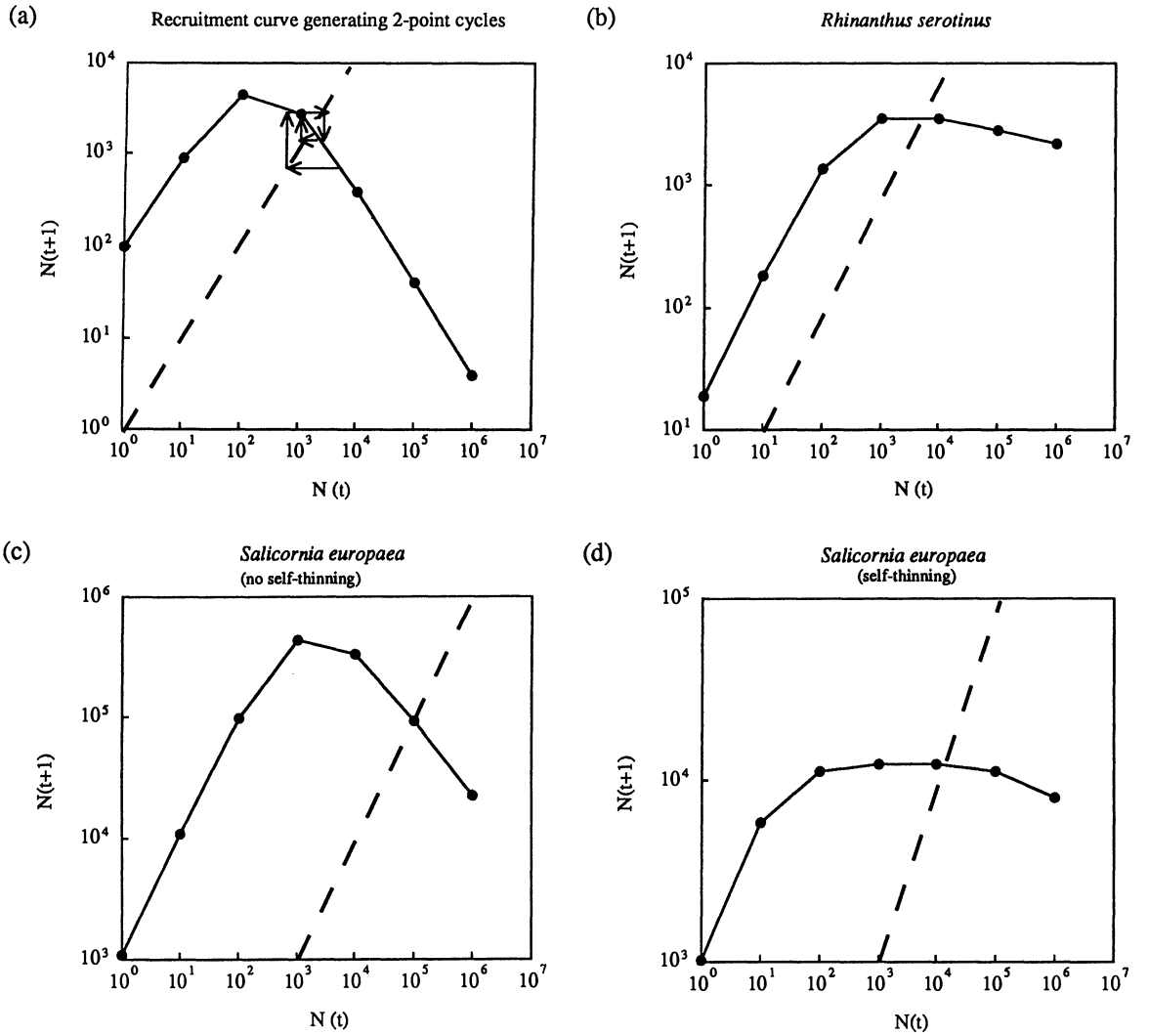

Fig. 1. Recruitment curves for (a) an 'ideal' population with oscillatory dynamics (equation 1, $\lambda = 100$, $a = 0{\cdot}005$, $b = 2$). The trajectory of the population is shown by arrows: (b) *Rhinanthus serotinus* (equation 1); (c) *Salicornia euroapaea* with no self-thinning (equation 1); (d) *Salicornia euroapaea* with self-thinning (equation 2). Parameters for the calculation of (b)–(d) from Watkinson & Davy (1985). The dashed line in each indicates $N_t = N_{t+1}$.

Rees & Crawley argue that the law of constant final yield should normally prevent the phenomenon seen in *E. verna* from occurring. This is not strictly correct, because the law applies to biomass, not to seed production. Whereas yield expressed as biomass is generally asymptotic with rising density, it is frequently parabolic for plant parts such as reproductive structures (Harper, 1977). When the law of constant yield does apply to seed yield, $b = 1$ in equation 1. For values of $b > 1$ the recruitment curve is humped.

In a review of the population dynamics of annuals Watkinson & Davy (1985) found $b > 1$ in two of seven populations. In one of these, *Rhinanthus serotinus* (ter Borg, 1979), the recruitment curve is humped, but the diagonal $N_t = N_{t+1}$ intersects the curve to the left of the maximum (Fig. 1b). In the other species, a low marsh population of *Salicornia euroapaea* (Jefferies, Davy & Rudmik, 1981), the shape of the recruitment curve and the dynamics of the population depend upon the presence of density-dependent mortality (self-thinning). When mortality is ignored (equation 1) the population should cycle (Fig. 1c). A mortality term $m\lambda N_t$ can be included in equation 1 to account for self-thinning (Watkinson, 1980):

$$N_{t+1} = \frac{\lambda N_t}{(1 + aN)^b + m\lambda N_t} \qquad \text{Equation 2}$$

Using an estimated value of $m = 8 \times 10^{-5}$ in equation 2 (Watkinson & Davey, 1985) reduces the hump in the recruitment curve, though it does not

remove it, and causes the diagonal to intersect the curve at a point where population stability is expected (Fig. 1d).

A negative intercept on the resource use/fitness graph is an inadequate test of the existence of a reproductive threshold. Furthermore, the existence of a reproductive threshold is not a *sufficient* condition to generate a hump in the recruitment curve. However, the question that originally motivated Rees & Crawley remains an interesting one. Are there fundamental differences between animals and plants that influence their population dynamics? The crucial issue is the assymetry of competition between large and small individuals in crowded populations, because this influences the shape of the recruitment curve (Watkinson, 1980). Plants and animals should indeed exhibit different dynamics, because plant competition for resources is inherently assymetric and competition among animals is not, unless they are territorial. This prediction is not based upon a distinction between modular and unitary organisms, but upon a difference between autotrophes and heterotrophes.

In strongly assymetric competition, equivalent to Nicholson's (1954) contest competition, winners take all. Large individuals suppress small ones and are unaffected by them. In symmetric competition, equivalent to Nicholson's scramble competition, individuals all receive some share of the limiting resource. Large individuals *are* affected by small ones. Symmetric competition, combined with the existence of a reproductive threshold, is destabilizing (Readshaw & Cuff, 1980).

Plants in crowded monocultures typically exhibit a highly skewed size frequency distribution with many small and few large individuals (Benjamin & Hardwick, 1986). Such distributions are generated by competition for light which is inherently assymetric because taller and larger plants interfere with smaller ones but not vice versa. By contrast, competition for below-ground resources tends to be symmetric and does not generate size inequality (Weiner, 1986).

I conclude then, that Rees & Crawley may be partially correct, and that plants are less likely to exhibit complex population dynamics than animals, but that this is because plants are autotrophic and compete for light, not because they are modular. There is no good evidence that modularity affects the existence of a size threshold for reproduction and Rees & Crawley's test does not address this question directly. Neither, I submit, is there any good evidence yet as to whether Rees & Crawley *or* I am correct that fewer plants than animals exhibit population cycles. Ideally, the detection of cyclic behaviour requires observation over many generations, backed-up by the construction of a recruitment curve which shows the required parabolic relationship with density (Symonides, 1983; Symonides *et al.*, 1986).

Because perennial plants have long generation times and habitats are often successional or disturbed, it is very unlikely that cycles will be observed in perennial populations, even where the conditions necessary to generate them exist. It is not surprising then, that all three recognized examples of plant population cycles are annuals (*E. verna,* Symonides *et al.*, 1986; *S. patula*, Wilkon-Michalska, 1976; *A. theophrasti*, Thrall, Pacala & Silander, 1989). In the last of these species Thrall *et al.* (1989) have inferred cyclic behaviour from a recruitment curve, but oscillations in the field were damped by seed dormancy.

For cycling to be reliably detected in the field, studies should last at least 5 years, but very few studies are as long as this. A comparison of recruitment curves between representative samples of univoltine insects and annual plants would be the best way to test the hypothesis that animal and plant populations have the potential to exhibit different dynamics. Whether this potential is realized can only be discovered by more long-term field studies.

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Do plant populations cycle?

The general question about whether field populations of annual plants exhibit cyclic or chaotic dynamics is both interesting and important. Silvertown believes that there are three examples of plant population cycles. We consider that none of these studies satisfactorily demonstrates population cycles, and we shall discuss briefly each of the three examples to point out what we regard as their main shortcomings.

Erophila verna

Symonides, Silvertown & Andreasen (1986) present three pieces of evidence which they suggest document regular two-point cycles.

1 In 20 quadrats observed over a 4-year period the seedling density appears to follow a regular two-point cycle. This small set of 20 cycling quadrats was carefully chosen, and as Symonides (1984) states: 'the studies . . . have been restricted to an analysis of natality only in the case of a very low and a very high density'. Data from a much larger study of 1600 quadrats studied for 7 years were not presented (Symonides, 1983a,b). It is therefore impossible to determine whether the data from the 20 selected quadrats are representative.

2 The number of transitions between low (1–4 seedlings), intermediate (5–10 seedlings) and high (11–56 seedlings) density quadrats is also given. These data are from 200 quadrats studied over 7 years (i.e. about 12·5% of the available data). Of these 200 quadrats, only those where *Erophila* was present for all 7 years were used in the analysis, so a further 30 quadrats that contained *Erophila* for 6 years or fewer were excluded from the analysis. Thus, the analysis presented in Symonides *et al.* (1986) is based on only 5% of the available data. It is important to note that at least 50% of the *Erophila* populations in their small sample of quadrats did not undergo two-point cycles, but went locally extinct. Thus, even in this small fraction of the available data the evidence for cycling is equivocal. We need a complete analysis of all 1600 quadrats, showing the number of quadrats that have persistent populations and, of those that are persistent, the proportion that are cyclic. This could then be compared with the expected number of cyclic quadrats calculated on the basis of an appropriate null hypothesis.

3 The third piece of evidence presented by Symonides *et al.* (1986) is a humped relationship between seedling density and seed production. This is not a sufficient condition for two-point cycles as demonstrated by Symonides *et al.* (1986) in their original paper. In order for two-point cycles to occur the fraction of seeds that survives to become seedlings must lie precisely between 0·5 and 1%, irrespective of weather conditions in any given year. Furthermore, their analysis assumes that *Erophila* does not form a seed bank, but Symonides herself (1984) has shown that, in the soil environment, seeds 'remain viable for 3–4 years'. The incorporation of a seed bank could stabilize the *Erophila* population as in the case of *Abutilon* (see below).

We suggest that the evidence of widespread cycling in *Erophila verna* is less than compelling.

Salicornia patula

Silvertown quotes an unpublished PhD thesis originally cited in Symonides (1988). We have not