The grasshopper model: Ecological dynamics far from absorbing states

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1 The problem

How can there be so much grass and so many grasshoppers? Resource competition models day that resources are limiting to reproduction:

$$\frac{dN}{dt} = r(1 - N/K) \tag{1}$$

What is the meaning of K?

1. $K = \epsilon R$ where ϵ is the efficiency of an organism in turning resource R into offspring; this implies entirety of resource is used up before dN/dt is negative.
2. $K = \epsilon \rho R$ where ϵ is as before and ρ is the proportion of the biomass of R available to the metabolism of the organisms.
3. $K = \epsilon \rho R$ where ϵ is as before and ρ is now interpreted as the probability of discovering a packet of available resource.

Problems with these interpretations (at least in the case of grass and grasshoppers):

1. Resources are abundant
2. All above ground biomass is available to metabolism yet we observe these resources are not depleted
3. Resources are easy to find

This implies grasshoppers are far from resource constraints and thus far from absorbing states (resources depleted and all grasshoppers extinct). Yet the system is "stable," i.e. there are no local extirpations of grass or grasshoppers though of course there are fluctuations in the total biomass of both. This suggests we need a new model.

2 Basics of the grasshopper model

1. Death from predation, disease, old age (but *not* starvation) are more important than resource limitation

2. satiation means per capita reproductive rate does not increase indefinitely w.r.t. resources

3. per capita death rate should be constant w.r.t. resources except in extreme case of near starvation conditions

4. predation should include density dependence because pray are harder to find when rare

5. in the extreme case where there's almost no resource then density dependence should hold for the primary consumers as well, i.e. there should be a term (a probability) s.t. d^2N/dt^2 is negative for very low resource levels or very low probabilities of resource discovery

3 Speciation when resources aren't limiting

1. occurs from dispersal limitation and geographic isolation

2. occurs from strong selection on ways to avoid predation/disease

3. occurs from sexual/social mechanisms

Note: all these speciation mechanisms are true for the very polyfagus grasshoppers along with rare cases of host switching discussed below

4 Speciation by resource switching when resources aren't limiting

The height of fitness peak is set by metabolic rate of species, not by amount of resource. Therefore the height of the peak is not relevant to selecting, rather the gradient of the peak is.

Host switching when resources are not limiting should thus be rare(?) as is observed in grasshoppers.

Note that if resources are patchy and organisms are dispersal limited then locally we should see density dependence and apparent resource competition thus opening up the classic selective mechanisms leading to speciation by host switching. The question is: do all clades that speciate by host switching specialize on rare hosts. The answer of course is no. And in fact these clades would have selective pressure to eventually switch to common hosts. Thus it seems more likely that such clades have metabolic pathways that require them to specialize, i.e. they have not discovered how to be generalists. Thus if they specialize and switch hosts and in the process speciate it is not necessary (although it is sufficient) for the host to be

rare. There is the other mechanism that they are constrained to specialize. Therefore, do these clades climb fitness peaks based the gradient of the peak as in the case of grasshoppers, and if so what is the consequence for the predicted rate of speciation if resources are not limited by specialization is metabolically required?