Reproductive decisions: Finding the best blend of sex and asex.

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Motivation: Life histories are the events and traits that determine life cycles of species in nature, and life-history related decisions often involve balancing trade-offs. Multicellular organisms expand clonally (i.e. increase the extent of genetically identical components) by adding tissue and sometimes by producing asexual propagules capable of developing into separate individuals--thus increasing their local control of space and other resources. This asexual expansion (asex) trades off against sexual reproduction in the short term but also increases the potential for subsequent sexual reproduction. Sex is thus the reproductive end product that is essential for surviving local extinctions and genetic dead ends through long-distance dispersal and genetic mixing. Males and females may generally differ in the way they balance the sex-asex trade-off.

Research Questions: How much sex and how much asex are optimal for males and for females in a population distributed across local habitat patches loosely connected by dispersing propagules (i.e. in a metapopulation)? How do these optima depend on an environmental disturbance regime capable of eliminating parts of patches and (less frequently) entire patches? How do the optima depend on productivity--expressed by the maximum possible local expansion rate? What is the relation between the sex ratio at the whole population or metapopulation level and the patch-level dynamics?

Methods: We built a computer simulation model using MATLAB programming software and used an alternating hill-climbing algorithm to find optimal subdivisions of reproductive effort into sex and asex for males and females separately. Because the optima are interdependent, this amounts to solving a game between the sexes. Here the optima maximize evolutionary advantage (i.e. fitness) across the entire metapopulation. We calculated the metapopulation sex ratio via extinction discounting of local patch dynamics (i.e. by taking expected patch persistence times into account) and illustrated these local dynamics using isocline methods (a graphical way of depicting trajectories of male and female abundances through time).

Results: We found (1) that males and females may differ considerably in their relative emphases on sex and asex; (2) that the two sexes generate both more sex and more asex at higher productivities but favor sex in more intense disturbance regimes; and (3) that local stable coexistence of males and females that compete for space is rare and is associated with relatively equal abundances of males and females at the metapopulation level.

Discussion: Sexual reproduction is a way of dealing with environmental variation and unpredictability in space and time, but asex is an essential means of potentiating sex. All evolutionarily successful multicellular organisms must be capable of achieving or approximating the best mix of these two reproductive modes, an ability enforced by natural selection. Interactions between males and females in nature, such as those considered here, generally

include elements of both cooperation and conflict, such that their life histories and other decisions are the outcome of games between the sexes.