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Population ecology is the section in introductory ecology courses that first intrigues students. In the following article, Professor Truman P. Young, Department of Environmental Horticulture, University of California, Davis has created a model to illustrate the characteristics of semelparity life history.

In our second article, Binney Girdler (Kalamazoo College), Stephen Trombulak (Middlebury College), and Ana Ruesink (The Nature Conservancy of Vermont), three collaborators on course-related research projects for students, have collaborated in writing an excellent guide for forming such partnerships.

THE POPPY PARADOX AND A NOVEL DERIVATION FOR THE DEMOGRAPHIC CONDITIONS FAVORING THE EVOLUTION OF SEMELPARITY

Judging by textbooks (Stearns 1992, Silvertown and Lovett Doust 1993, Bulmer 1994, Begon et al. 1996, Barbour et al. 1998, Freeman and Herron 1998, Ricklefs and Miller 2000, Krebs 2001) and dozens of course web pages, the evolution of semelparity is a popular topic in undergraduate and graduate ecology and evolution classes. Semelparity/iteroparity is an elegant life history dichotomy that yields to fairly straightforward demographic modeling with an interesting history (Cole 1954, Charnov and Schaffer 1973, Young 1981, Young and Augspurger 1991) that has produced quantitative tests in natural populations (Young 1990, Lesica and Young, *in review*). The traditional approach to modeling this dichotomy mathematically is through comparing intrinsic rates of increase of genotypes with higher fecundity but no adult survival (semelparity), to genotypes with lower fecundity but some adult survival (iteroparity). I offer here a derivation of this model that is more intuitive, and, I suspect, that may be more realistic as well. I assume here a basic understanding of the evolutionary modeling issues involved (to brush up, see the above references).

I was standing in my garden the other day looking at the recruitment of a second generation of California poppies that I had planted. This species (*Eschscholzia californica*) occurs as both annual and perennial forms (Hickman 1993). Commercial seed is often a mixture. Of the seeds that I broadcast-planted last year, most turned out to be of the annual genotype. I got to wondering about the competition between these two forms across generations. If there are a fixed number of suitable slots (establishment sites) for poppies in my garden (or at any site), then in each generation the number of slots that open up will be equal to the number occupied by annuals last year (all of which died), plus those of the perennials that died. These available slots will be filled by a random subset of the seed rain of the previous generation (let's assume no seed dormancy). This is most likely how semelparity evolved in nature—in cases where overall population size remained constant ($\lambda = 1$), and there was competition between the two genotypes for living sites.

Take the simple case where all the perennials survive from year to year. Each year, all of the sites occupied by the annuals become available, and at least some of these are filled by seeds from the perennial genotypes. In the next generation, there will be more perennial genotypes. Eventually the entire population will be perennial. This will be true regardless of the initial frequencies of the two genotypes, absolute fecundities, or the fecundity advantage of semelparity.

This conceptual model produces the inverse of Cole's paradox, which I call the Poppy Paradox. Whereas Cole suggested that a semelparous genotype would be favored if it produced even one more seed than a perennial genotype, the reasoning above suggests that no matter how large the fecundity advantage of semelparity, it will lose out to iteroparity. Rather than asking "Why are not all plants semelparous?", we are left asking "Why are not all plants iteroparous?"

In each case, the paradox is solved by understanding that no population experiences 100% survivorship all the time. Charnov and Schaffer (1973; see also Young 1981) provided the solution for Cole's paradox, and I will do it here for the Poppy Paradox. As long as there is at least some adult mortality of the perennial genotype, there will exist a theoretical fecundity advantage of semelparity that ensures that the annual genotype produces enough seeds to replace itself fully (or even to gain sites). The greater the mortality of the perennials, the less this fecundity difference needs to be, and the more likely that semelparity will be favored. We can quantify the relationship between the two either through simulation or through an analytical derivation.

First, the simulation. Imagine that you start with 100 perennial and 100 annual genotypes, and 10% of the perennial genotypes die each year. At the end of the first year, 110 sites open up (all of the annual sites, and 10 of the perennial sites). If each perennial genotype produces 10 seeds, how many seeds does each annual genotype need to produce to ensure an equilibrium? Because there are 110 slots available, and the annual genotypes need to fill 100 of them, they need to produce 100/110 of the total seeds. Because the perennial genotypes have produced 1000 seeds in total, the annual plants need to produce 10,000 in total, or 100 apiece, in order to achieve 10,000/(10,000 + 1000), which equals 100/110. You can do this with any starting numbers of the genotypes and any number of seeds per perennial genotype, and the answer is the same if the perennial has 10% mortality; each annual needs to produce 10 times as many seeds, on average, as each perennial in order to break even. If more seeds are produced, the annual genotype eventually excludes the perennial genotype. Fewer, and the perennial genotype eventually excludes the annual genotype.

However, the answer does change if you change the adult survivorship rate of the perennial. If there is 20% perennial mortality, the annual needs to produce five times as many seeds. If there is 50% perennial mortality, the annual needs to produce twice as many seeds. Students can try different combinations of perennial mortality, initial proportions, and absolute seed set to confirm this pattern and its generality. The emergent result is that for the annual to be as successful across generations as the perennial, it needs to produce $B_A/B_P = 1/(1 - p)$ times as many seeds, where B_A equals the fecundity of the annual genotype, B_P equals the fecundity of the perennial genotype, and p equals the annual survival of the perennial genotype (and $1 - p$ is its yearly mortality).

This result can also be generated analytically. Let B_A/B_P be the fecundity advantage of semelparity (as above). Also, let m be yearly adult mortality of the perennial ($m = 1 - p$), N be total population size, and s be the proportion of the population that is annual. Then Ns is the number of annuals in the population and $N(1 - s)$ is the number of perennials in the population. Each year $Ns + mN(1 - s)$ plants die and open up the same number of slots for new seedlings.

The proportion of those slots that were annuals is

$$\frac{Ns}{Ns + mN(1-s)} .$$

The proportion of next year's seeds that come from the annuals is

$$\frac{NsB_A}{NsB_A + N(1-s)B_P} .$$

For the annual genotype to maintain its numbers in the population, these two terms must be equal:

$$\frac{Ns}{Ns + mN(1-s)} = \frac{NsB_A}{NsB_A + N(1-s)B_P}$$

$$\frac{s}{s + m(1-s)} = \frac{sB_A}{sB_A + (1-s)B_P}$$

$$\frac{1}{s + m(1-s)} = \frac{B_A}{sB_A + (1-s)B_P}$$

$$sB_A + (1-s)B_P = sB_A + m(1-s)B_A$$

$$(1-s)B_P = m(1-s)B_A$$

$$B_P = mB_A$$

$$\frac{B_A}{B_P} = \frac{1}{m} = \frac{1}{1-p} .$$

This is the same result as that of Charnov and Schaffer (1973) and, later, Young (1981) for situations where $\lambda = 1$, and the perennials flower in their first year and every year thereafter. As iteroparous adult mortality (m) approaches zero, B_A/B_P approaches infinity, making it impossible for semelparity to evolve: the Poppy Paradox. Note that the result lacks a term for juvenile survivorship. This is because, by fixing population size and perennial adult survivorship, juvenile survivorship is also fixed relative to fecundity (see Young 1981). The result is also independent of N, s, and the absolute values of B_A and B_P.

In nature, the attainable values of the relative fecundity advantage of semelparity (B_A/B_P) are in the range of 2–5 fold (Young 1990, Young and Augspurger 1991), which corresponds in the model to adult survivorship rates of 50–80%. Populations of perennial plants with adult survivorships less than this will be prone to evolving semelparity, especially if they have certain predisposing traits (see Young and Augspurger 1991).

I hope that this novel approach to the semelparity model will provide a more accessible conceptual and mathematical explanation.

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GUIDELINES FOR PARTNERSHIPS IN APPLIED ECOLOGY AND EDUCATION

An approach to ecological education advocated by an increasing number of teachers is a move away from "cook book" laboratory and field exercises and toward involving students directly in group or individual research projects with "real-world" applications. The theory behind such a pedagogy is straightforward. First, students are more likely to become active, rather than passive, participants in the learning process if they feel *engaged* in a scientific investigation, and engagement is far more likely if students do not feel as if they are just going through the motions to reach a predetermined answer (Leonard 1991, Howard and Boone 1997, NAS 1997). Second, with increasing attention being given by students to the connections between science and society (Gordon 1998), they are more likely to actively participate in projects that address questions in applied ecology, particularly conservation and natural resource management, and that have clearly observable applications. Incorporating such research projects into the classroom is often most readily achieved through a partnership between an educator, who directs the work of the students and develops the pedagogical structure of the project, and a conservation practitioner, who provides the rationale and background for the project and helps students see the importance of the work.

At least, this is the theory. The practice of developing such a curriculum, however, can be another matter entirely. The time required to plan and organize educational exercises with real-world application, as in the work of conservation practitioners who work for natural resource organizations/agencies, is far greater than educators normally imagine; the cultures and constraints of educators and practitioners can be radically different, leading to challenges in communication and meeting expectations on both sides; and when curricula involving such partnerships fail to work, they can fail *spectacularly*.

However, we strongly believe that the educational benefits of such research projects dramatically outweigh the costs, and with only a little forethought and awareness, all of the risks can be reduced. Together, we have 25 years of experience incorporating individual and group research projects that involve partnerships with natural resource organizations/agencies into undergraduate curricula. Over these years, we have developed several guidelines that help make the experience more successful for everyone involved—students, teachers, and practitioners—and lead to both better education and natural resource management.

1) Aim for long-term collaborations rather than those that last for only one semester or quarter. Natural resource organizations/agencies, especially those in the government, have planning horizons that are longer than a year, and a short-term collaboration will almost always involve cutting corners for expediency, and is unlikely to result in a positive experience for the students or a useful product for the organization/agency partner.

2) Do not give up working with a particular organization/agency after contacting only one person and failing to reach an agreement. This kind of partnership relies on shared education and research goals, and not every combination of teacher and practitioner is going to achieve that mutual understanding.

3) Do not try to carry out a new and different project each time. Rather, build on earlier projects. Three-quarters of the work involved in integrating applied projects into a curriculum is in the initial planning and site reconnaissance; it takes at least one class to get all the logistical problems worked out.

4) Allow adequate time for advance planning. As mentioned in suggestion (1), organizations/agencies may establish their work priorities up to a year in advance. Only by working with a long planning horizon can a good fit be found between the kind of project that will work for the teacher and the kind of project that is important to the natural resource organizations/agencies.

5) If students are novice scientists, as is typical in introductory classes, have them work in groups to tackle small pieces of a larger project for which data have already been collected. This makes it easier for students to connect with their projects and allows them to develop their skills without jeopardizing the entire project. For example, in an introductory applied conservation biology course, two students collected data on malformations in frog populations at sites that had been previously sampled by a state agency; the students were able to utilize established protocols and analyze their data in a larger context.

6) At the beginning of the project, have the organization/agency partners interact with students in the classroom and/or in the field, and to the extent possible, have this interaction continue throughout the course. Hearing about an issue from someone who lives and breathes it every day, instead of an academic who merely reads about it, is the best possible motivation for students. This is true even if the teacher *does* work directly on the issue; students become much more motivated about a project when they interact with someone for whom the project is a central part of their employment. For them, it brings the issue to life. The practitioner also benefits by having an on-going opportu-

nity to shape the project and make sure that it meets its objectives. However, it is important that the students be made aware of the boundaries to what they can expect from the practitioner. In particular, the amount of time that a practitioner has available for the project will nearly always be much less than students may be used to having from their instructors, leading to conflict if this issue is not directly addressed from the outset.

7) If you want to give the students some flexibility in selecting their own projects, yet still want them to address a larger applied issue of interest to an organization/agency partner, the teacher and practitioner should create a list of possible project ideas prior to the start of class. Without a list of possible topics to fall back on, many students will try to head off in unproductive directions.

8) If the project has enough flexibility, allow students to work on as wide a range of taxa as possible, or use as many different approaches to a single organism as possible. They can amaze you with the level of interest that they already have in different kinds of organisms, from plants to soil microbes to salamanders; their personal interest in particular organisms is a powerful tool for helping them develop a personal interest in the project. Be cautious, however, about organisms that create impossible time constraints. For example, at high latitudes, projects that focus on migratory birds, or mammals that hibernate, are likely to fail simply because the study organisms will not be available when the students need them to be.

9) Build a "final presentation" into the work plan. This works best if the presentation is made to one or more practitioners who can use the results of the research project, and if it is structured in the form of students making and justifying recommendations. We have successfully done this in many different partnerships, and students consistently consider it one of the most meaningful and important assignments they get while they are students.

10) Only take on a project whose size matches the students' available time. Projects that require 24-hour continuous sampling, for example, are less amenable than those that involve samples collected over a longer but less intense period.

11) If a project involves repeated sampling, add something new to the experience each time to minimize the complaint that "we did this already." Students, in general, will not want to come back to the same place week after week without "learning" something new. Build in interim evaluations or progress reports to help keep them motivated.

12) Do not use "cookbook" science language, especially for nonscience majors. In general, avoid the use of the term "lab" entirely; refer to the projects as "research programs" or "case studies" to which they are contributing data. Let them experience real-world science as a means to get credible answers to questions, not as a tangle of jargon.

13) Encourage opportunities for advanced or exceptional students to follow up on group research with more in-depth studies in subsequent semesters or quarters. Practitioners often find that the best data and the best value for their participation in these partnerships have come from such extensions to the original research plan.

14) Follow through with the organization/agency by providing data, reports, presentations, and feedback. Practitioners become involved in partnerships because they have a real need for results. If they are to see a long-term value in working with students and educators, the fruits of the partnership need to cycle back into their work in a meaningful way.

Hands-on exercises that involve such partnerships have the additional educational benefit of showing students that the application of ecological knowledge to solving management problems involves collaborative efforts among people with different skills, and that, although good science is critical, effective communication skills are equally important when applying the results of a scientific investigation. When provided with the opportunity to apply ecological ideas to the real world, students are both motivated to learn and rewarded by having done something useful. Natural resource organizations/agencies gain from the partnerships in several ways, including acquisition of useful data, generation of new project ideas from pilot data, and increased public interest in agency activity.

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