INT. J. SCI. EDUC., 2003, VOL. 25, NO. 1, 35–55

An examination of problem-based teaching and learning in population genetics and evolution using *EVOLVE*, a computer simulation

Patti Soderberg, Department of Biology, Beloit College, 700 College Street, Beloit, WI 53511, USA; e-mail: bioquest@beloit.edu; Frank Price, Hamilton College, 198 College Hill Road, Clinton, NY 13323, USA; e-mail: fprice@hamilton.edu

This study describes a lesson in which students engaged in inquiry in evolutionary biology in order to develop a better understanding of the concepts and reasoning skills necessary to support knowledge claims about changes in the genetic structure of populations, also known as microevolution. This paper describes how a software simulation called *EVOLVE* can be used to foster discussions about the conceptual knowledge used by advanced secondary or introductory college students when investigating the effects of natural selection on hypothetical populations over time. An experienced professor's use and rationale of a problem-based lesson using the simulation is examined. Examples of student misconceptions and naïve (incomplete) conceptions are described and an analysis of the procedural knowledge for experimenting with the computer model is provided. The results of this case study provide a model of how EVOLVE can be used to engage students in a complex problem-solving experience that encourages student meta-cognitive reflection about their understanding of evolution at the population level. Implications for teaching are provided and ways to improve student learning and problem solving in population genetics are suggested.

Introduction

The National Science Education Standards emphasize that students in the natural sciences should develop an understanding of the nature of science, which includes an appreciation of science as a human problem-solving endeavour and epistemological understanding of the origin and development of scientific knowledge (National Academy of Science 1996). The National Academy of Science (1998) also noted widespread misconceptions about evolution and emphasized that understanding evolution is essential to understanding what is and is not science (see also Gallup 2001). Unfortunately, despite the best attempts of teachers to insure that all students gain an understanding of evolutionary concepts, even highly educated students misunderstand aspects of evolution (Greene 1990). For example, Bishop and Anderson (1990) and Brumby (1984) have documented that college and medical students, respectively, use Lamarkian explanations to describe evolutionary phenomena.

The study of genetics is central to understanding how evolution occurs. However, despite its importance, genetics is considered difficult to teach (Johnstone and Mahmoud 1982; Finley *et al*. 1992) and difficult to learn

International Journal of Science Education ISSN 0950–0693 print/ISSN 1464–5289 online © 2003 Taylor & Francis Ltd
http://www.tandf.co.uk/journals
DOI: 10.1080/09500690110095285

(Stewart 1982). With respect to populations genetics specifically, this important part of evolutionary theory is rarely taught in high school biology classes, as is evidenced by its exclusion in most biology textbooks (Swarts *et al*. 1994). When population genetics is taught, students typically dislike learning about Hardy–Weinberg equilibrium as they frequently find it confusing, boring, and irrelevant to their lives (Eichinger and Nakhleh, 2000).

The National Academy of Science has also emphasized the importance of problem-based or inquiry learning. Unfortunately, students do not often receive such opportunities. For example, a survey of 90 lab exercises published in nine top-selling laboratory manuals showed that only two of the exercises required that students pose a question for investigation, and only 16 of all of the laboratory exercises asked students to formulate a hypothesis (Germann *et al*. 1996).

Researchers have documented that computer-based laboratories can enhance student learning in science (Nakhlek and Krajcik 1993) and lead to more positive attitudes toward learning (Ybarrondo 1984). Computer simulations and tools can provide increased opportunities for students to learn to think like scientists and can result in providing students with a greater understanding of epistemological issues related to the growth of scientific knowledge (Cartier and Stewart 2000). The use of such simulations can have a positive effect on student cognition, self-esteem, and behaviour (Johnson and Stewart 1990). In addition, the use of computer simulations and tools for teaching population genetics can help improve graphing skill and interpretation of graphical knowledge (Stuessy and Rowland 1989).

The knowledge used by biologists to solve problems in microevolution consists of two types: (1) conceptual knowledge – such as knowledge about genes, alleles, dominance, and natural selection; and (2) procedural knowledge – such as knowledge about algorithms and general heuristics used to solve complex problems. Understanding of expert and novice cognition and behaviour during problem-solving sessions provides useful information for assessing and improving student learning. Educational research in population genetics is important for helping educators design more effective evolution curricula, to increase our understanding of student learning in evolution, to develop a better theoretical understanding of evolution as a problem-solving endeavour, and to design more inquiry-based pedagogical activities.

Teaching and learning are complex processes that should involve continual reflection. Best practice is not intrinsically perfect. Accounts of teaching practices that are connected to theory in order to critique educational practice, make appropriate changes, and justify those changes in a rational and logical way show elements of best practice. Classroom-based reports such as this one, provide examples of best practice and situate those practices in theory through a detailed analysis of teaching that is research based. Research reports that include rich descriptions of classroom practices are useful for reform as teachers can use such documents to reflect on their own practice, emulate good practice, assess the results of the changes, and justify or criticize their actions accordingly.

The purpose of this study is to provide an example of best practice by documenting a lesson about microevolution using *EVOLVE,* a Macintosh software simulation (Price and Vaughan 1993, 1994, 1995, 1996, 1998) combined with an analysis of teaching and learning. The research questions for this study were: What are the benefits of having students learn about population genetics and evolution, experimental design, and modelling using a computer simulation? How can simulations be used to reveal student preconceptions and misunderstandings and help them develop a more sophisticated understanding of Mendelian genetics, population genetics, and of evolution? What is the desired procedural and conceptual knowledge that students should have when using *EVOLVE* to investigate evolutionary phenomena at the population level? How can teachers aid students in improving understanding and problem solving using simulations such as *EVOLVE*? This study describes a sample lesson where students learned about population genetics and evolution and the effect of natural selection on the frequency of alleles in a population through experimental investigations using *EVOLVE*. The lesson serves as a basis for reflective practice to provide suggestions as to ways student learning and problem solving in population genetics can be improved.

Method

EVOLVE

EVOLVE enables students to learn about population genetics by manipulating selection, genetic drift, and migration (gene flow) and observing the effects on a population over time. It models evolution in a single-locus, two-allele system under various selection pressures. A user can create a sample population by entering values for the initial size of the population and the proportional frequency of the two alleles in the starting population (figure 1). Next, the user sets the 'carrying capacity' or largest size the population can reach as well as the size the population will return to in each generation that the population exceeds its set 'carrying

Figure 1. *EVOLVE* enables users to experiment with various starting populations of organisms by changing the parameters of a single locus, two allele mating system. A model can be run over time and the results of the simulation displayed on a line graph where population numbers or frequencies are on the X axis and the Y axis is number of generations.

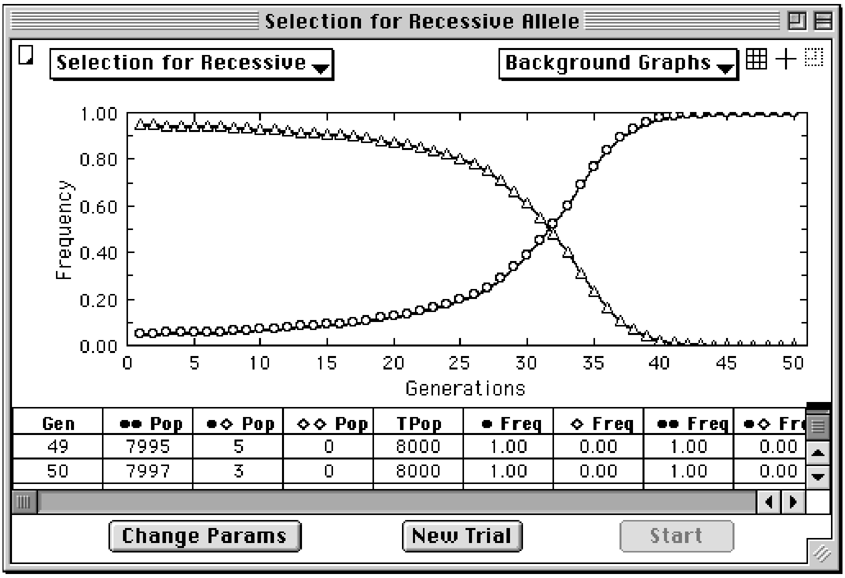

Figure 2. The graph shows frequencies of alleles over time. The table shows actual numbers and frequencies in each generation. The bullet allele frequency (open circles) increased from 0.05 in generation one to become the most common in generation 32 and almost reaches fixation after generation 40. The diamond allele (triangles) declined from 0.95 to almost zero. The table shows there were still 3 heterozygotes in generation 50.

capacity' (found under the 'Genetic Drift' button). The fitness of a genotype is dependent on the survival rate and reproductive success of those organisms compared with organisms with the other two genotypes. The fate of the sample population can be modelled over time by designating the number of generations to be simulated. The model assumes that each generation of organisms can only breed with other organisms of the same generation. After each run of the system under the initial starting parameters, the frequencies of the alleles and number of organisms of each of the three genotypes in the population are plotted over time (figure 2).

EVOLVE is a useful tool for helping students to learn about population genetics and evolution because students can pose 'what if?' questions about a population of interbreeding organisms, alter the characteristics of the starting population and the relative fitness of the alleles within a population, and investigate the consequences. Basic knowledge of Mendelian genetics is required to use *EVOLVE*. Students can use *EVOLVE* to investigate the effects of selection, drift, and gene flow on hypothetical populations.

Data collection and analysis

We used four methods to gather data: (1) interviews with professors and students; (2) class observations; (3) audiotapes of think-out-loud, problem-solving sessions with an expert; and (4) a request to see the focus professor's written teaching philosophy.

Seven professors from six different undergraduate institutions were interviewed about their use of *EVOLVE* in their undergraduate biology courses. Of these seven, one was chosen to serve as a focus of the study based on the amount of experience using *EVOLVE* and his willingness to be observed teaching and problem solving. The interviews of the other six professors were used to confirm the findings related to student learning and problem solving using *EVOLVE*. The focus person was asked to pose a question using *EVOLVE* that he would use with his students and solve it out loud. The audiotape of the problem-solving session was transcribed and used as the basis for subsequent interviews in which the professor was asked to explain and clarify his actions in the context of how and why he used this problem with students. In addition, the problem-solving transcript was analysed using procedures described by Collins and Stewart (1987) based on information-processing theory in order to discern the general procedures used by experts to investigate evolutionary phenomena at the population level and to serve as a model of desired performance.

The professor who served as the focus was asked to teach a class using *EVOLVE* where the students would solve the problem that the professor had solved during the audiotaped problem-solving session. As the professor was no longer teaching undergraduates at the time of the study, he was asked to model 'best practice' to other instructors participating in a workshop who were interested in learning how to use *EVOLVE* in order to observe how a lesson could be structured and to gather additional data on why the professor felt this lesson and his pedagogy valuable for students. In addition, it was assumed that any difficulties experienced by the instructors in this class would be likely to occur in a class with advanced secondary or undergraduate students and that the instructors were more likely to express any difficulties they encountered. Two consecutive classes were observed. Careful notes were kept and were used to construct a description of the lesson based on a composite of the two lessons. The description of the class was provided to the professor for verification. The professor made revisions to the description to arrive at a description that he felt represented best practice. This description was analysed in the tradition of Lincoln and Guba (1985) and Woolcott (1994). The findings were confirmed by comparing the interviews (Seidman 1991) of the six other professors. Semi-structured interviews were also conducted with five undergraduate biology students and were analysed to identify misconceptions that emerged when the students used *EVOLVE*.

A description of the lesson is included below, followed by an interpretive discussion of the professor's actions and educational philosophy as well as insights gained from the interviews of students and other professors and the problem-solving transcript. The study concludes with suggestions for improving student learning and problem solving in population genetics and provides a model for teaching microevolution from a problem-solving perspective.

A Description of the Lesson

The following narrative describes a 3-hour class where the students learn to use *EVOLVE* and answer a question about evolution. 'P' and 'S' refer to professor and student respectively. S, S1, S2 refer to different students and do not always represent the same student.

Professor Hill (pseudonym) begins the lesson by telling the students that the goal of the class is to answer the following question: Does evolution of a dominant allele proceed faster than that of a recessive allele with a comparable phenotype? He asks the students to work in small groups of two or three. The students start *EVOLVE* on their computers while the professor projects the screen showing where they will enter starting variables for their experiments (figure 1). As they learned to use the program, the professor asked them to think about what it means to say that evolution happens faster. 'In other words,' the professor clarified, 'we are asking, what is the effect of increasing the selection pressure? What is the effect when you have selection operating more strongly on a population?'

He asks them to think about a species of birds with alleles for long (symbolized by •) and short (symbolized by ◇) wings. Birds with long wings are able to fly further and faster and are better able to escape predators and find food. Long-winged birds have a higher fitness and are more common (95% of the gene pool) than the allele for short wings (5%). Next, they are to suppose that a storm has blown a large flock out to sea and 8.000 colonize an island with no predators. They will treat the island population as their experimental population. On the island, winds are strong and birds with long wings tend to get blown out to sea and die; those that survive expend energy fighting the wind and lay fewer eggs. The short-winged birds walk more, expend less energy, and lay more eggs. On the island, the short-winged birds have a higher fitness. They will assign long-winged birds an average 22% survival rate from hatchling to adulthood and short-winged birds a 30% survival rate. The long-winged birds will average five hatchlings and the short-wings 8.1.

Professor Hill notes the defaults for the number of generations (50), initial population (8,000, initial diamond allele frequency = 0.95), and genetic drift (9.999 and 8,000) fit the scenario and don't need to be changed. He tells the students there are four evolutionary forces that can change a population: natural selection, genetic drift, gene flow and mutation. He explains that mutation was the only evolutionary force that could not be modelled in *EVOLVE*. They would begin by only manipulating values associated with natural selection. Professor Hill walks to the board and says they will initially treat the bullet allele as recessive. The homozygous recessive genotype will have short wings and the other genotypes will have long wings. He asks the students to enter the following variables for their first experiment:

	••	•◇	◇◇
Survival rates	30	22	22
Reproduction rates	8.1	5	5

The students ask how a dominant gene could have lower fitness, or a lower frequency. He tells them to remember that dominance is defined by the phenotype that the heterozygote and one of the homozygotes exhibit. He tells them to click on the 'Done' button. 'Before you hit the start button, I want you to try to visualize in your mind what you think will happen' (see figure 2).

Professor Hill points out that there are variations among their experiments. 'There is some variation, or genetic drift, between all of your experiments.' He shows them how to scroll down to the end of their data table. The teams compare their results. Some have one heterozygote, some have two, some have three. The teams of students compare the number of heterozygotes that still remain after 50 generations. Some have one heterozygote, some have two, and some have three. A student comments, 'We were all starting with the same data, yet we got different results?'

Professor Hill replies, 'Yes, because of genetic drift and because there is randomness built into the program.' He then asks, 'If we increase the strength of selection, what will happen?' If an identical flock is blown onto an island with stronger winds, how can you change *EVOLVE*'s parameters to increase the strength of selection? Students suggest decreasing the reproductive rate of the diamonds, or their survival rates, or both. After a pause, a third student suggests they could increase rates for the short-wings.

Professor Hill states that all of these will work, but suggests the third is better for their experiments. Decreasing the rates for the diamonds could produce a declining population and that might affect results. To eliminate that variable, he writes on the board:

	●●	●◇	◇◇
Survival rates	40	22	22
Reproduction rates	8.1	5	5

He asks the students to predict what they expect to see before they run this new trial: 'O.K., at what generation did the [dominant] allele go extinct for you?' The student teams call out the generation number when extinction occurred in their model: '46', '37', '37', '35', '37', '47', '36'.

The professor points out that again this variation is expected owing to genetic drift. His students observe the phenomena of genetic drift before they learn the label. The students describe the differences between their results, noting the curves of the two experiments were generally similar, but the changes occurred more quickly in the second, with the alleles' curves crossing 11–13 generations earlier, and the diamond allele went extinct in generations 28–32 (see figure 3).

Now that the students knew how to change the selection pressure Professor Hill returned their attention to the original research question, ''Does evolution of a dominant allele proceed faster than that of a recessive allele with the same phenotype?'' He tells the groups to discuss the question and come up with three things: an answer, either yes or no; a prediction of how the results will differ; and an experimental design to test their hypothesis.

Hill records each team's answers and paraphrases predictions on the board and puts tick marks for duplicates:

Yes	*No*	*Predictions: what to look for*
✓✓✓		Dominant curves will cross in an earlier generation
	✓	Homozygous recessive will become extinct sooner, but heterozygotes will remain
✓✓		Deleterious allele will become extinct sooner
✓		Curve for dominant will be above recessive

'These are typical. Students often will look for landmarks. The 50 per cent point where curves cross is common. Or, they pick a specific generation and say the frequency of the advantageous allele will be higher in that generation.'

Professor Hill asks the students to talk about experimental design. He uses the conversation to guide them to the following numbers:

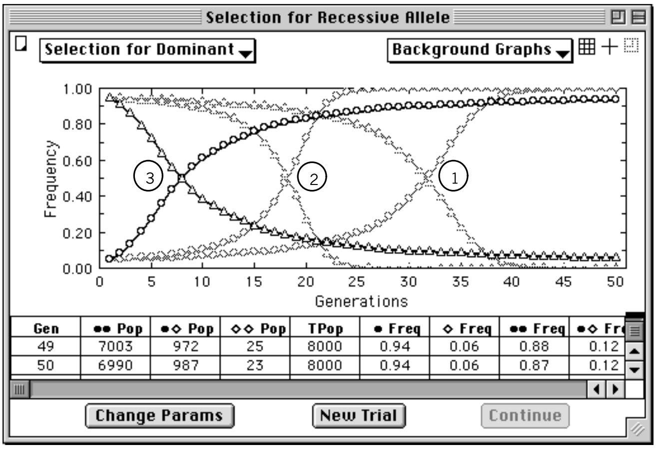

Figure 3. The results for the three experiments described in the lesson. The circled numbers refer to runs one through three of the model. The data for the third curve seen in the foreground can be found in the table below the graph. Note that the phenotypes in 1 and 3 are identical, but the pattern of inheritance differs (recessive in 1 and dominant in 3).

Title	*Selection for dominant*		
	●●	●◇	◇◇
Survival rates	22.0	30.0	30.0
Reproduction rates	5.0	8.1	8.1

He points out that the advantageous genotype should start from a low frequency, and writes on the board:

Initial allele frequencies ● = 0.95 ◇ = 0.05

Next he asks the class to help rewrite the table to show selection for the recessive. Some students become confused at this point because they suggest numbers that switch the bullet allele recessive to dominant. The professor helps them to see that it is easier to reverse the numbers of the homozygotes keeping the bullet allele as the recessive:

Title	*Selection for recessive*		
	●●	●◇	◇◇
Survival rates	30.0	22.0	22.0
Reproduction rates	8.1	5.0	5.0
Initial allele frequencies	● = 0.05	◇ = 0.95	

He summarizes their options. ‘So, you can keep the allele frequencies and swap the pattern of inheritance, or you can keep the pattern of inheritance and swap the initial allele frequencies.’

S: ‘To show more change, you have to flip the allele frequencies and start with a high recessive.’

> P: 'If you want to show selection against the recessive. But I want all of you to be the same for today. O.K., Let's set up a new trial.'

He tells them to use the variables in the last table. The students change the parameters and run the new trial (figure 3, curve 3).

> P: 'O.K. what did you see?'

> S: 'Selection against a recessive [pause]. You got rid of a lot of the recessives, but you can't get rid of them all. They are still in the heterozygotes.'

Two students at the front are animatedly discussing their screen, trying to resolve their confusion about what they are seeing. Professor Hill notices their confusion and asks what their problem is. He clarifies that this group thought that at generation 50, the data points for each allele frequency would be close together and that the recessive allele frequency would be above, or higher than the frequency of the dominant allele.

> P: So you thought that at generation 50 it should look like this.' He draws on the board (figure 4).

Another student comments:

> S: 'Wait, I've lost sight [pause], my prediction was that the dominant trait would become extinct before the recessive. [Pause] but extinction did not occur in either.'

The students express a concern over the way the problem statement was worded. They are concerned with what is meant by 'proceeds faster'.

> S: 'Let me explain the second ambiguity. The slopes of the curves are different than if you look at generation 50.'

> P: 'Is selection against the dominant relatively fast or slow to begin with?'

The students are not in agreement about how this question should be answered.

> P: 'At the beginning, selection against the recessive proceeds faster at first, but at generation 50, selection against the dominant proceeds faster. The mathematician would want to look at slope. What should *you* do?'

> S: 'Add another curve.'

Professor Hill says that they need to look at something population geneticists call 'delta q', or change in frequency from one generation to the next. He says that they can export their data to spreadsheet, compute the derived data and produce new graphs. To save time, he shows them what the curves will look like on the board (see figure 5).

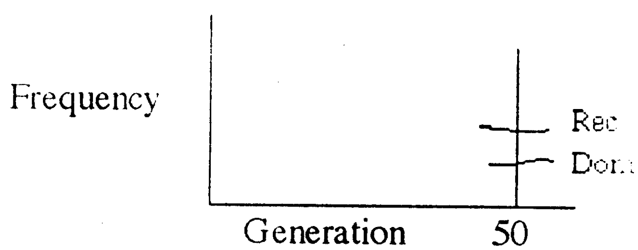

Figure 4.

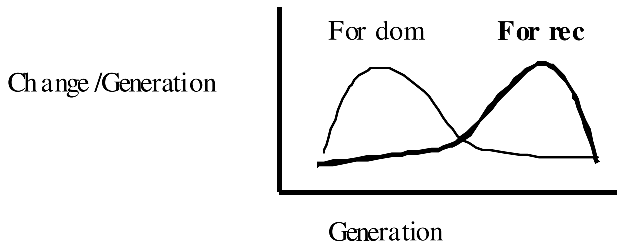

Figure 5.

A student asks which peak is higher. Professor Hill says that the bottom line is that the 'for recessive' curve is slightly higher. Selection favouring a recessive is faster than selection for a dominant with the same phenotype.

> P: 'Why don't the dominants take over? Perhaps a better wording would have been "Does selection against a dominant allele eliminate it faster than selection against a recessive allele?" I have asked the question both using "against" and using "for". No matter how I phrase it, people usually answer that the dominant will be faster.'

The professor concludes the lesson by commenting on the perceptions associated with language.

> P: 'Dominant. The connotation of the word is faster, stronger, fitter. The social connotations of language tend to overwhelm the technical meaning of the word. Think about a blind salamander. A blind salamander that is wimpy, thin-limbed, and blind *is* stronger, better in a cave.'

Professor Hill and the students discuss examples such as Huntington disease where the recessive genotype is advantageous or sickle cell anaemia where the heterozygote is advantageous. The Professor comments that these would be good problems to explore the evolution of alleles in populations.

> S: 'Evolution. I don't think of it as evolution.'
>
> Another S: 'I think of evolution as change in frequency.'
>
> A third S: 'I couldn't figure it out—evolution of the dominant allele [pause] but, it's already there! I think of evolution as mutation and change, not as in natural selection, even though we're supposed to think of it this way.'

Discussion and analysis with implications and recommendations for improving student understanding and problem-solving performance

In this section of the paper, the transcripts of the class descriptions, individual problem-solving, think-out-loud sessions using *EVOLVE*, and interviews with professors and undergraduate biology students are analysed as to the:

(1) *philosophical goals and pedagogical methods* used by biology educators to assist and guide students who are learning population genetics and evolution by solving a problem with *EVOLVE*;
(2) *conceptual issues* that emerge when solving a complex problem in population genetics and evolution using *EVOLVE*;

(3) desired *problem-solving* strategies that lead to successful performance and conceptual problems that impede progress; and
(4) *recommendations* of strategies that can improve student learning and performance in similar lessons.

Philosophy, pedagogy and EVOLVE

The issues that the novice problem solvers struggled with while using *EVOLVE* provide insights as to the ontological assumptions inherent in teaching and learning evolutionary concepts in advanced high-school- or college-level introductory biology courses. The problem-solving strategies are analysed as to the general and domain-specific strategies that resulted in successful problem solving. The follow-up interviews with the professor who taught the observed classes and the additional professors who use *EVOLVE* in a similar way with students were used to elucidate and verify student conceptions and problem-solving strategies. The results of this analysis provide:

(1) a model of how *EVOLVE* can be used to teach about population genetics and evolution; and
(2) implications for student learning and problem solving.

During the class session, students were asked to design experimental models to test whether selection against a dominant allele would proceed faster than the same selection pressure against a recessive allele with a comparable phenotype. Professor Hill is a pseudonym for the person who taught the lesson described in this paper.

Professor Hill feels there are two main purposes for having students use *EVOLVE* to answer the problem regarding the relative speed of evolution on two alleles. His objectives are: (1) to help the students confront their assumptions about concepts in evolution, especially with respect to dominance; and (2) become successful problem solvers. His beliefs about teaching and learning are constructivist in nature. He believes that students enter his classroom with many talents, beliefs and experiences, which all shape what, how and why the student will learn. He strongly disagrees with teacher-centred educational systems that expect passive acceptance of information by students. Professor Hill views his students as novice problem solvers. He feels that more will be gained if his students learn via problem solving as opposed to simply learning about problems that have been solved by other scientists (textbook knowledge) or for problem solving where they learn algorithmically to solve certain types of problems. Professor Hill recognizes the importance of learning the factual information in textbooks and the use of algorithms to solve problems, but he also realizes that students can perform satisfactorily on certain types of tests with only a rote understanding of concepts. He wishes to help his students develop an understanding of biological phenomena and theory that is lifelong rather than an ephemeral artefact of cognitive survival skills learned by participation in traditional schooling. He recognizes the essential tension between his need to provide students with guidance and his need to provide freedom to try things on their own. He writes in his philosophical statement:

> Attempting to give students experience with research is fraught with dangers. Experiment labs tend to be either too rigidly laid out, with obvious results and interpretations (in which they are really demonstrations), or are so vague that students flounder because they lack theoretical background and practical experience. Most

> student-designed experiments have design flaws and do not yield sufficient data with variances low enough to permit valid conclusions. Even if there are no design problems, well-executed experiments are usually beyond first year students; anything except very simple equipment tend to get in the way of conceptual understanding.
>
> I believe understanding statistics is the best way to learn the nature of science. Statistical tests explicitly require alternative hypotheses, one of which is refuted, and the nature of statistical significance emphasizes the tentative nature of science. Implicitly, the point is made that biology requires quantification, and biology majors start to learn what will become a major professional tool. Liberal arts students also benefit from even this brief exposure to statistics. We are all continually barraged with statistics, so some understanding of them is useful to citizens in general.

His own intuitions are consistent with current learning theories in education. He understands that if knowledge is conceptually connected in a deeper, more substantive schema, it is more likely that the knowledge will be stored in long-term memory. Deeper knowledge is more useful in solving complex problems and can be used to explain the biological knowledge associated with successful algorithmic problem solving behaviours (Chi *et al*. 1988).

Problem-based lessons enable Professor Hill to assess student learning formatively through conversations about problems, hypotheses, and solutions. These conversations enable him to identify and correct or prevent misconceptions by helping students to reflect metacognitively on their knowledge in order to recognize their assumptions. He also wants his students to learn about the process of science at the same time they are learning science content. Professor Hill is committed to educating for deep understanding; his primary objective is to insure that each student develops a semantically rich schema that includes both structural and procedural knowledge within a biological field's domain. He wants assessment of student knowledge to check for rote understanding of knowledge, meaning that a demonstration that the material has been memorized to the extent that questions can be answered, but without an understanding why the answer is correct. He also wants to assess deeper, more meaningful learning, meaning a demonstration that the student can answer a question correctly and demonstrate an understanding of why a response is correct. He strives to use formative and summative assessment that checks for deeper understanding while minimizing the chance of students passing the exam using only knowledge gained through rote memorization.

Addressing conceptual issues using EVOLVE

Professor Hill's use of *EVOLVE* enables his students to design and run simulated experiments to solve problems in evolutionary biology by asking 'What would happen if . . . .' The value of the lesson described in this study was that it enabled Professor Hill to bring out student assumptions related to dominance and rate of evolution in a population and confront their assumptions with evidence from modelling experiments that contradict common expectations. Professor Hill's intuitive beliefs about how students learn have developed as a result of many years of experience in teaching biology. He does not use the language of educational theories to label and describe his beliefs, but it is possible to describe these beliefs with models of learning found in the education literature. Professor Hill views instruction as a process of changing students' misconceptions to conceptions that are scientifically acceptable. In a conceptual change model of instruction (Posner *et al*. 1982) student's misconceptions must first be explicitly identified and challenged. Next, the students must understand the alternate (scientifically acceptable) explanation or, in other words, perceive it as plausible, intelligible, and fruitful. Finally, for meaningful and long-lasting learning, the students must see how the concept relates to other knowledge in science or to solving problems. For example, Professor Hill recognizes that misconceptions about genetics concepts are common and can have a rational basis.

> I often point out, and ask the question, why did you think the dominant advantageous allele would evolve faster? And usually they say something about fitness that is about physical fitness. If you are big and strong, then you are dominant against somebody who is smaller or weaker. Dominance seems to be about being faster, bigger, heftier, more macho. So they kind of bring the social constructs, the social connotations of the terminology. We are not using dominance in the way that it is being used in the health class or in the locker room, or in the psychology lab. We are using it as a technical term in evolutionary biology and that is a very different word, so people are misled by a technical term that looks very comfortable.

Professor Hill wants his students to understand that dominance is a description of the relationship between two different alleles and cannot be assessed from the abundance or the fitness of a particular phenotype. In a two-allele, single-locus system, the phenotype of the heterozygote will be the indicator of the dominant allele.

A primary pedagogical strategy of teachers who are teaching for conceptual change is to use a demonstration, a hands-on manipulation event, or film footage depicting a particular phenomenon, where they know from experience that the students will make an observation that will contradict their existing beliefs. The use of discrepant events can result in meaningful learning where a student must accommodate his knowledge structure in order to account for (explain) the intellectual discrepancy. Professor Hill does not use the language of educators to call such tactics discrepant events, as he has not had formal training in education. However, he does use this instructional strategy with his students. He simply describes this strategy as events that make the students say, 'Hey, that's not doing what I thought would happen', or 'Oh, I didn't think about it *that* way before.' In the case of naive assumptions related to the concept of dominance, he typically uses the example of cave-dwelling salamanders as a 'discrepant event' to promote discussion between him and his students. His specific intent is to confront and conceptually challenge commonly held views of dominance as phenotypes with attributes such as strength, speed, and power, or other similar attributes. Professor Hill uses a blackboard to illustrate his example in an *EVOLVE*-style interface. He writes on the board:

	●●	●◊	◊◊
S	50	50	80
R	8	8	8

and points out that in this case 'eyeless' is the recessive phenotype. 'Here,' he emphasizes, 'is an example that is contrary to conventional notions of fitness. In this case, the fittest organism is the one that has no eyes and is pale.' The dominant phenotype that has the characteristics one would normally associate with better fitness such as strong eyesight and less sickly looking coloration is not the fittest in this ecosystem. He stresses, 'Dominant doesn't say more fit or less fit. Dominant simply says pattern of inheritance.'

Professor Hill also checks to see whether or not his students are constructing a schema of concepts that will enable them to communicate effectively and accurately about the phenomena they are studying. The students must be able to recognize that advantageous/disadvantageous, extinction/fixation, selection for/selection against are opposites and realize when they can be interchanged to make statements with the same meaning. For example, 'If you flip the [research] question around, it was initially formulated as selection favoring a dominant versus selection favoring a recessive. You can say the same thing by saying selection for a dominant is selection against a recessive. And selection for a recessive is selection against a dominant.' He avoids confusion through careful and consistent use of terminology and also by explicitly pointing out how two statements can appear quite different, yet still mean the same thing. Consistent and unabbreviated use of language when teaching can alleviate confusion. For example, some of the PhD biologists observed in these two lessons did not understand what the professor meant by 'strong sel' as they entered 'strong cell' as the title of the run of one of their models.

The question that the professor asked his students to solve is simple, but the students view it as complex as the answer can vary depending how a group of students decides to define and measure evolution. Selection for a dominant phenotype in a population with a small number of dominant alleles will occur faster when the allele frequency is under 50 per cent and slower when the frequency becomes greater then 50 per cent. In other words, the rate of change will be greater for a dominant allele prior to a 0.5 frequency and less after this point over a series of generations. Conversely, selection against a dominant allele that occurs at a high frequency in a population will occur slower over time when the allele frequency is under 50 per cent and faster over time when it is above 50 per cent. The question's strength is that it enabled Professor Hill and his students to have an extensive dialogue about meanings of dominance and recessiveness and how they viewed them when examined at familial and population levels.

To help his students understand the dynamics of selection over a period of time, Professor Hill summarizes their research results in the form of a table during a class discussion (table 1).

Problem-solving strategies and common student misconceptions that impede problem interpretation

Johnson (1996) found that novices and experts performed similarly solving new problems where they had no previous experience solving a problem of that type, despite the larger knowledge base of the experts about genetics in general.

Table 1

	Rate of change below 50%	*Rate of change above 50%*	*Complete fixation or extinction?*
Selection for a dominant	Faster	Slower	No—recessives still exist in population
Selection against a dominant	Slower	Faster	Yes—fixation eventually occurs

Geneticists are educated to solve each problem in a particular way. As one professor observed, ‘Traditional models of evolution have you enter selection coefficients. Students do not approach it this way.’ Therefore, it makes little sense to begin students, who are new to population genetics problems, with learning experiences that start by presenting them problems where they must reason from selection coefficients, cause, to subsequent effects. This may produce rote learning. If students are asked to reason from effect to cause, that is from deviations from the Hardy–Weinberg norm to calculations of selection coefficients, the learning outcomes will be different.

Slack and Stewart (1990) found that individuals new to a type of problem, tend to be unsystematic in their exploration of a problem. In genetics, problem-solving ability can be improved by having novices reflect meta-cognitively on successful problem solving in a cognitive apprenticeship to elucidate the heuristic strategies (Slack and Stewart 1989). To determine the strategies used to solve problems successfully using *EVOLVE*, Professor Hill was asked to solve the same problem that he used in the lesson. A tape recording was made as he thought out loud, while solving the problem. This tape was transcribed, then analysed to look for the heuristics that enabled him to solve the problem successfully. These heuristics can be provided to help students when they are not making progress when using *EVOLVE*. Such heuristics can help lead to increased problem-solving success:

(1) Pose a question.
(2) Think of a real or imaginary example to establish a context for the problem.
(3) Make a prediction (generate a hypothesis) before each run of the model.
(4) Test the hypothesis more than once under the same conditions.
(5) Identify landmarks by which the graphs can be analysed (cross-over points, a particular generation, point of extinction or fixation, or slope).
(6) Compare the experimental results of the first set of runs with a second set of experimental runs based on a new model that is the opposite of the first.
(7) Compare data to landmarks from first experimental run.
(8) Pose new questions, if any.
(9) Run additional experiments if needed.
(10) Make conclusions.

In addition to the procedural knowledge, experts also have a conceptual knowledge base that includes recognition of naive and common misconceptions in their population genetics schema. They recognize concepts that may function as barriers to successful problem solving by novices. For example, when Professor Hill helps his students to interpret graphs, he is explaining and checking for feedback about their conceptions of equilibrium, steady state, and HW equilibrium and fixation. Professor Hill also notes that students often hypothesize that the dominant allele will reach fixation faster or cannot go extinct. Interviews with other professors confirmed this observation. Other examples of problematic, or incomplete knowledge that were identified through semi-structured interviews of undergraduate students using *EVOLVE* are summarized in table 2.

For example, the following statements were made by two undergraduate students during interviews about the phenomena that they were observing or explaining in *EVOLVE*:

Table 2. Common student misconceptions observed when using *EVOLVE.*

Concept	*Naive or incomplete assumptions about concept*	*Problem with conception*
Natural Selection	Selection is a negative pressure.	Selection can be negative, positive, or neutral.
Equilibrium	Allele frequencies are 50-50.	Equilibrium occurs when frequencies reach a steady state. HW equilibrium has a different meaning.
Stability	Runs of a given model will be identical if no changes are made to the parameters.	Genetic drift is ignored. The student's mental model of natural selection is deterministic.

S1: 'Oh, I thought that the alleles would be equal, that is 50–50, when it reached equilibrium.'

S2: 'When the alleles reach a steady state, then the system is in Hardy–Weinberg equilibrium.'

Each student used a scientifically unacceptable definition of concepts of equilibrium and steady state in the context of population genetics. Courses where students share and justify experimental conclusions and are encouraged to reflect meta-cognitively on their knowledge claims have a greater potential for increasing and deepening conceptual understanding of difficult topics.

Recommendations of strategies to improve student understanding in similar lessons

Before students can begin to use the *EVOLVE* simulation to formulate a solution to the question, they must understand the concept of natural selection. Examples of natural selection that students commonly recall involve only the mechanism of survival. It is less common to find students who recall examples that depend solely on reproduction rate and rare to find students who can recall examples that include both reproduction and survival. Before using *EVOLVE*, it is advantageous to have students solve problems where they must think about fitness by considering both survival and reproductive success. The following problems are recommended examples that are useful for helping students assess their knowledge about fitness:

Problem 1. Based on the following information alone, which of the following birds can be said to have the greatest fitness?

A. Bird 1 lays 3 eggs, 3 hatch, 2 reproduce.
B. Bird 2 lays 4 eggs, 3 hatch, 2 reproduce.
C. Bird 3 lays 5 eggs, 4 hatch, 4 reproduce.
D. Bird 4 lays 7 eggs, 6 hatch, 3 reproduce.
E. Bird 5 lays 9 eggs, 3 hatch, 3 reproduce.

Problem 2. Determine the overall fitness for the following genotypes: A, B, C, D and E of the same species and arrange the genotypes in order of decreasing fitness (1 = most fit, 5 = least fit).

	Survival to maturity	Average number of offspring
A	0.90	1.0
B	0.40	3.0
C	0.50	1.5
D	0.50	2.0
E	0.75	0.9

In order to understand how evolutionary knowledge develops about populations of organisms, students need to be able to test hypotheses. *EVOLVE* is a valuable tool for helping students to think like population geneticists because it enables students to see changes in gene frequencies over time and to make comparisons and conclusions based on different starting populations and parameters. By modelling hypothetical populations students can develop a conceptual understanding of how evolutionary forces cause the proportions of a particular phenotype to change in a given population. Professor Hill stresses the need for students to formulate and test hypotheses throughout the class. He stops the class at key points and asks the students to make a prediction.

> 'Before you hit the start button, I want you to try to visualize in your mind what you think will happen.'
>
> 'You should be mentally predicting what you will see in the curves.'
>
> 'I want you to answer the question as either yes or no. Then, I want you to think about experimental design, how would you test this? And I want you to make a prediction first.'

When he told the class to visualize expected results in their heads, the students, even the PhD biologists, tended to hit the start button immediately, exhibiting little or no thinking time. To change this behaviour, the professor always requests the students to indicate their predictions by raising their hands. He records the consensus of each small research group on the board in the form the number of 'yes' and 'no' answers. Then he allows the groups to run the simulation. In addition, Professor Hill makes a point of calling each run of the simulation an 'experiment'.

Pedagogically, it is important to have students look critically at their assumptions about concepts associated with evolution (Hewson and Hennessey 1992, Jimenez-Aleixandre 1992). For example, even the highly trained biologists in this study had difficulty thinking about evolution as changes in populations of organisms, rather than as changes in individual organism when solving a complex problem. It is well documented that quite young children tend to believe in the inheritance of acquired characteristics (Kargbo *et al*. 1980; Hackling and Treagust 1984; Clough and Wood-Robinson 1985a), but tend to display a more consistant understanding of mechanisms of biological adaptations by the time they are 16 or older (Clough and Wood-Robinson 1985b). However, the persistence of beliefs that adaptations are due to some grand overall purpose or that adaptation is a conscious process, dependent on the organism's needs was still obviously present in the 16-year-old group in the latter study. These teleological and anthropomorphic explanations were even found to persist in first-year university students with an A-level biology background (Brumby 1979). Such research emphasizes the need to carefully explore student explanations of mechanisms for phenomena such as the blind cave salamander mentioned at the end of Professor Hill's lesson. In addition, *EVOLVE* can help students recognize that an understanding of natural selection includes a view of natural selection as mortality and reproduction rates. All of the professors interviewed stated that their students tended only to describe examples of natural selection related to mortality when asked to define fitness. Several professors noted that students also tended to view the reproduction rates as absolute rather than as averages and that it was important to address this problem explicitly.

Finally, it is important to point out the shift in thinking that is required for understanding in microevolution. Students typically are first taught about evolution as mutation and selection. Understanding and success in solving problems in micrevolution requires that one extend the mutation-selection model and think about evolution as changes in the gene structure of a population over time. The conceptual shift is difficult. As one biologist stated at the end of the lesson, 'I couldn't figure it out—evolution of the dominant allele [pause] but, it's already there! I think of evolution as mutation and change, not as in natural selection, even though we're supposed to think of it this way.' Therefore, it is critical to have explicit conversations with students to draw out mental models about individuals, traits, mutation, and selection in connection with population definitions of evolution.

Conclusion

The purpose of this study was to document and critique a lesson where students engaged in inquiry as a means of gaining greater familiarity with concepts in evolution and population genetics and to improve their reasoning skills necessary to support knowledge claims about populations of organisms. It is hoped that as a result of this study, biology educators will be able to improve student understanding of evolution, particularly with respect to an epistemological understanding of the origin and development of their knowledge, enabling students to make a Darwinian synthesis between genetics and evolution.

This study describes a lesson where students learned that evolution can be measured as the rate of change of allele frequencies in a population using a computer simulation called *EVOLVE*. The professor used the lesson to help students to meta-cognitively examine their understanding of concepts in population genetics and evolution and recognize common misconceptions related to dominance. The lesson helped the students shift from thinking about genetics from an individual or familial level to a population level, a necessary conceptual framework that is key to successful problem solving in population genetics and microevolution. The desired problem-solving strategies used by an expert in the field were presented in this paper and provide a model of desired problem solving when posing and solving problems using *EVOLVE*. In addition, the logic of commonly held misconceptions and the persistence of teleological and anthropomorphic explanations of adaptive mechanisms that are often present in student explanations of genetics and evolutionary phenomena are explored in the analysis of the lesson. The researchers conclude that the benefit of using *EVOLVE* is that it provides situations for the students to practise, demonstrate, and articulate their understanding of concepts such as dominance, drift, equilibrium, steady state, Hardy–Weinberg equilibrium, and fixation. It is recommended that educators who use *EVOLVE* should situate problems by providing an example, real or imagined, that the students can relate to and to provide them with supplementary problems that help students assess their understanding of fitness. Finally, students should be encouraged to exhaust a problem space systematically by manipulating only one variable at a time and to always make a prediction prior to each run of the simulation.

This study increases awareness of the possible misconceptions and naive conceptions that can be expressed by students when using *EVOLVE* so that educators can be prepared to encourage and support student ideas, therefore increasing opportunities to help students recognize problematic statements, beliefs, procedures, and conclusions. It also provides recommendations of strategies for improving student learning and problem solving in population genetics and evolution. In addition, educators tend to focus on students and their conceptions, but this lesson reveals that even highly competent biologists can struggle with the subtleties associated with thinking about biological phenomena in a complex problem space. Intuitive beliefs can persist and appear in certain classroom situations despite personal knowledge of why such beliefs are not scientifically acceptable and educators should remind themselves of the importance of patience and tolerance when working with students as they struggle to find solutions to complex problems. Finally, it is hoped that the results of this study encourage the development of more problem-based, genetics and evolution courses or units where students have the opportunity to participate in articulating and justifying their ideas and conclusions through the process of inquiry.

Acknowledgements

Major support for this research was provided by a grant from the Howard Hughes Medical Institute, Grant No. 71196523302. Special thanks to Steve Fifield, Kathy Greene, Peter Hewson, John R. Jungck, Jim Stewart and Chris Young for their comments and suggestions during the preparation of this manuscript, and to Marion Meyer and Jean Heitz for the sample problems they use to help students assess their understanding of fitness.

References

Bishop, B. A. and Anderson, C. W. (1990) Student conceptions of natural selection and its role in evolution. *Journal of Research in Science Teaching*, 27, 415–427.

Brumby, M. (1979) Problems in learning the concept of natural selection. *Journal of Biological Education*, 13, 119–122.

Brumby, M. (1984) Some misconceptions and misunderstandings perpetuated by teachers and textbooks of biology. *Journal of Biological Education*, 18, 201–206.

Cartier, J. L. and Stewart, J. (2000) Teaching the nature of inquiry: further developments in a high school genetics curriculum. *Science and Education*, 9, 247–267.

Chi, M. T. H., Glaser, R. and Farr, M.J. (eds) (1988) *The Nature of Expertise* (Hillsdale, NJ: Erlbaum).

Clough, E. E. and Wood-Robinson, C. (1985a) How secondary students interpret instances of biological adaptation. *Journal of Biological Education*, 19, 125–130.

Clough, E. E. and Wood-Robinson, C. (1985b) Children's understanding of inheritance. *Journal of Biological Education*, 19, 304–310.

Collins, A. and Stewart, J. (1987) A description of the strategic knowledge of experts solving realistic genetics problems (MENDEL Research Report No. 1) (Madison, WI: University of Wisconsin).

Eichinger, D. C. and Nakhleh, M. B. (2000). Evaluating computer lab modules for large biology courses. *Journal of Computers in Mathematics and Science Teaching*, 19, 253–276.

Finley, F.N., Stewart, J. and Yarroch, W. L. (1992) Teachers' perceptions of important and difficult science content. *Science Education*. 66, 531–538.

GALLOP (2001) Substantial numbers of Americans continue to doubt evolution as an explanation for origins of humans. Online. Available: http://www.gallup.com/poll/releases/pr010305.asp

Germann, P. J., Harkins, S. and Auls, S. (1996) Analysis of nine high school biology manuals: promoting scientific inquiry. *Journal of Research in Science Teaching*, 33, 475–499.

Greene, E. D., Jr (1990) The logic of university students' misunderstanding of natural selection. *Journal of Research in Science Teaching*, 27, 875–885.

Hackling, M. W. and Treagust, D. (1984) Research data necessary for meaningful review of grade ten high school genetics curricula. *Journal of Research in Science Teaching*, 21, 197–209.

Hewson, P. W. and Hennessey, M. G. (1992) Making status explicit: a case study of conceptual change. In R. Duit, F. Goldberg and H. Niedderer (eds), *Research in Physics Learning: Theoretical Issues and Empirical Studies* (Kiel, Germany: IPN), 176–187.

Jimenez-Aleixandre, M. P. (1992) Thinking about theories or with theories? a classroom study with natural selection. *International Journal of Science Education*, 11, 541–553.

Johnson, S. (1996) *Student as Scientist: The Strategies Used in the Process of Model Revising Problem Solving in Genetics*. Unpublished doctoral dissertation, University of Wisconsin–Madison.

Johnson, S. K. and Stewart, J. (1990) Using philosophy of science in curriculum development: An example from high school genetics. *International Journal of Science Education*, 12, 297–307.

Johnstone, A. H. and Mahmoud, N. A. (1982) Isolating topics of perceived difficulty in high school biology. *Journal of Biological Education*, 14, 163–166.

Kargbo, D. B., Hobbs, E. D. and Erickson, G. L. (1980) Children's beliefs about inherited characteristics. *Journal of Biological Education*, 14, 137–146.

Lincoln, Y. S. and Guba, E. G. (1985) *Naturalistic Inquiry* (Beverly Hills, CA: Sage Publications).

Nakhlek, M. B. and Krajcik, J. S. (1993) A protocol analysis of the influence of technology on students' actions, verbal commentary, and thought processes during the performance of acid-base titrations. *Journal of Research in Science Teaching*, 30, 1149–1168.

National Academy of Science (1996) *National Science Education Standards* (Washington, DC: National Academy Press).

National Academy of Science (1998) *Teaching about Evolution and the Nature of Science* (Washington, DC: National Academy Press).

National Academy of Science (2000) *Inquiry and the National Science Education Standards* (Washington, DC: National Academy Press).

Posner, G. J., Strike, K. A., Hewson, P. W. and Gertzog, W. A. (1982) Accommodation of a scientific conception: toward a theory of conceptual change. *Science Education*, 66, 211–227.

Price, F. and Vaughan, V. (1993, 1994, 1995, 1996, 1998) *EVOLVE*, In J. R. Jungck, J. Calley, N. Peterson, J. Stewart, E. Stanley, P. Soderberg and V. Vaughan (eds), *The BioQUEST Library* [CD-ROM], Vols I–V (San Diego, CA: Academic Press).

Seidman, I. E. (1991) *Interviewing as Qualitative Research* (Columbia, NY: Teachers College Press).

Slack, S. and Stewart, J. (1989) Improving student problem solving in genetics. *Journal of Biological Education*, 23, 308–312.

Slack, S. and Stewart, J. (1990) High school students' problem solving on realistic genetics problems. *Journal of Research in Science Teaching*, 25, 237–254.

STEWART, J. (1982) Difficulties experienced by high school students when learning basic Mendelian genetics. *The American Biology Teacher*, 44, 80–89.

STUESSY, C. L. and ROWLAND, P. M. (1989) Advantages of micro-based labs: electronic data acquisition, computerized graphing, or both? *Journal of Computers in Mathematics and Science Teaching*, 8, 18–21.

SWARTS, F. A., ANDERSON, R. O. and SWETZ, F. T. (1994) Evolution in secondary school biology textbooks of the PRC, the USA, and the latter stages of the USSR. *Journal of Research in Science Teaching*, 31, 475–505.

WOOLCOTT, H. F. (1994) *Transforming Qualitative Data* (Thousand Oaks, CA: Sage Publications).

YBARRONDO, B. A. (1984) *A study of the effectiveness of computer-assisted instruction in the high school biology classroom*, Report No. SE046309. (East Lansing, MI: National Center for Research on Teacher Learning). ERIC Document Reproduction Service No. ED265015.