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Evolution for undergraduates: fostering critical thinkers

K A Bryant & M C Calver

School of Biological Sciences and Biotechnology,
Murdoch University, South St, Murdoch, WA, 6150

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Abstract

The process of evolution underpins all in biology, directs research and provides a unifying explanation for the history and diversity of life. The study of evolutionary biology draws on many disciplines (from molecular biology to ecology to palaeontology), and has applications in numerous areas, such as medicine, conservation, and agriculture. How then do we use evolution to train university undergraduates in a meaningful way, and what do we want them to learn? There are many aspects of evolution that could be taught at the undergraduate level, and content will vary depending on the course-context. Some basic components include the evidence for evolution, microevolution, speciation and macroevolution. However, teaching evolution offers exciting opportunities to convey more than just content. Evolutionary biology immerses students in the *process* of science and should encourage them to think critically and to carefully analyse concepts, problems and evidence. It offers students nearing graduation the opportunity to draw together their learning across different areas in biology, asking them to synthesize their thinking and appreciate how problems in evolution can be analysed with multidisciplinary tools. In this paper we argue the importance of teaching evolution and justify its place in the teaching curriculum by providing examples of its wide applications, and by using case studies to illustrate the value of inquiry learning in teaching evolution at all undergraduate levels.

Keywords: evolution, evolutionary biology, inquiry based learning, scientific method

Introduction

According to Murdock (1945, as cited in Wilson 1998), all human cultures studied have accounts of the origin of biodiversity. Modern biologists are in overwhelming agreement that the best explanation of how existing biodiversity arose is evolution, in which all living species are descendants of the earlier ones and share a single common ancestor. From the early 18th century onwards evidence has accumulated steadily to support the evolutionary viewpoint, with an explosive increase of convincing molecular evidence during the late 20th and early 21st centuries (see, for example, Nardi *et al.* 2003; Tarlinton *et al.* 2006; Endicott *et al.* 2009).

Given the natural human curiosity about the mechanisms behind the origin and diversity of life, as well as the agreement of almost all biologists that the explanation lies in evolution, we believe that it follows naturally that evolution should be an important part of teaching biology at all levels of our education system. It may therefore come as a surprise to some that evolution is a recent addition to the curricula in some Western countries (Chinsamy & Plagányi 2008; Sanders & Ngxola 2009), or that in some cases there are strong campaigns to remove evolution from biology curricula (Bleckmann 2006).

We believe that researchers and teachers in the biological sciences should always look critically at the subject matter they present to ensure that it remains factually accurate, up-to-date and relevant to the needs of students in contemporary society. Knowledge is expanding at a rapid rate, yet University degrees remain fixed at three-year lengths, so there is great competition for space in a crowded curriculum. It is helpful if material in the curriculum performs multiple functions to facilitate the breadth of objectives that students need to achieve within the short time of their degrees. Justifying the teaching of evolution within this scenario requires answers to three important questions. They are:

1. *Why teach evolution?* – how do we justify the teaching time when so many exciting biological developments are jostling for a share of students' time?
2. *What should we teach?* – exactly what parts of a dynamic and expanding discipline should be selected for the undergraduate curriculum at its different levels?
3. *How should we teach it?* – what examples and pedagogical techniques are appropriate to make the subject relevant and interesting for modern students?

In this paper we give our answers to all these questions, in the hope of providing resources to colleagues teaching evolutionary biology for the first time and giving important background to educational researchers wishing to use the teaching of evolution as a case study. Given the breadth of evolutionary biology, we are unable to explain all background biology and evolutionary theory for each example that we present. However, we feel that a wide breadth of examples is critical to illustrate the breadth and the diversity available for teaching. Therefore while our descriptions are often short, we do provide primary and secondary references so that interested readers may follow up topics in greater depth. We also present some examples as more detailed case studies, to illustrate the teaching elements within them. Our examples are necessarily selective and inclined toward our personal interests in evolutionary ecology rather than other equally important areas such as palaeontology.

Why teach evolution?

The theory of evolution unifies modern biology

Undergraduate students studying biology or related disciplines will study the diversity of life on Earth, looking in detail at the different taxonomic groups, and comparing how they live and function in their specific environment. This taxonomic understanding is very important for all biologists. However, knowing *what* biodiversity is out there is only one level of understanding of the biological world; delving into questions about *why* that biodiversity exists, takes scientific minds to the next level. Studying evolution attempts to answer some of the most fundamental questions that humans can ask about the natural world, including:

Where did all the diversity come from? – as Samways (1994) points out, we know many physical constants in the natural world with great certainty, yet we cannot state confidently how many different species of life are on Earth. We do know, though, that there are a great many and have a good idea of the relative abundances of different groups. How was all this diversity formed?

Why are organisms like they are? – why, for example, do cetaceans breathe air when they live exclusively in aquatic environments, whereas most other aquatic vertebrates use gills?

Why do they do what they do? – in many mammals, males compete for access to females. In contrast, in Mormon crickets females compete for access to males (Gwynne 1981). Why should this be?

As Dobzhansky (1973) observed ("Nothing in biology makes sense except in the light of evolution"), evolution unites all biology in answering these questions. It can be thought of as a play unfolding within a theatre of ecology in which human beings themselves are included in the cast (Groom *et al.* 2006). The theory of evolution explains a great array of seemingly otherwise unrelated facts, from the universality of the DNA code amongst all living things, through to changes in the genetic make-up of populations over time, the similar biogeographic distributions of similar organisms, and the order of appearance of animal taxa, such as fish, amphibians, reptiles and mammals, in the fossil record. In that way, it provides a cohesive and unifying foundation for all of the life sciences.

As a result, evolution is studied using multidisciplinary tools, such as molecular biology, population genetics, population ecology, embryology and development, taxonomy and phylogeny, biogeography, palaeontology and studies in speciation, comparative anatomy, behaviour, physiology and biochemistry. Undergraduate units in evolution cannot attempt to offer technical training in each of these specialist areas, although they may offer training in one or two, if these are of common relevance to the student cohort. Ultimately evolution provides a framework to synthesize students' previous knowledge and provides an understanding of how each field of study can be applied to answer universal questions in biology.

Evolution exemplifies the scientific method

A further reason for teaching evolution is to illustrate the scientific method in action through inquiry-based learning, by which students discover knowledge for themselves by applying scientific methods rather than being shown passively (Finn *et al.* 2002). Alters & Nelson (2002) observed that this type of approach "….presents science as a process of critical thinking that provides a model for critical thinking elsewhere in the student's life."

In particular, studies in evolutionary biology require both observational and experimental approaches. Studies of comparative anatomy or of a series of fossils represent very good examples of observational science because there is no experimental manipulation, no control and no independent replication. However, predictions can be made on the basis of theory and tested through structured observations. Biogeography and the fossil record provide good examples of this approach in action (see, for example, the discussion of Antarctic paleoecology in Coyne 2009, pp. 102–103).

Evolutionary biology also provides numerous opportunities to illustrate the principles of experimental methods to test hypotheses. The classic textbook example has long been the case of industrial melanism in the moth *Biston betularia* in the United Kingdom. In Kettlewell's (1973) original experiments, dark and light morphs were exposed on different backgrounds. Their differing vulnerability to predation by birds in terms of their contrast to the background was demonstrated (for a review of more recent developments in this example, see Ridley 2004). Variations of this exercise are still practised with high school and undergraduate students using both field based (Barker 1983) and computer based activities (Gendron & Staddon 1984; Calver & Wooller 1998).

A key point that should be noted in the example above is that the work begins with a hypothesis, requires experimental and control treatments (given by characteristics of the backgrounds and the objects or shapes displayed against them) and needs adequate replication in the sampling to allow convincing tests of the original hypothesis. If desired, statistical analysis can also be taught in such exercises when students process their data. At the very least, students can also practise presentation techniques by using tables and graphs in written reports describing their experiments.

Understanding evolution has many practical applications

Any teacher of modern students is familiar with the catch cry: 'what is this all good for?'

Fortunately, evolutionary thinking applies to many different fields. For example, students of conservation biology should be aware that long-term conservation of biodiversity requires that we also conserve the process that renews it: evolution. This requires, amongst other

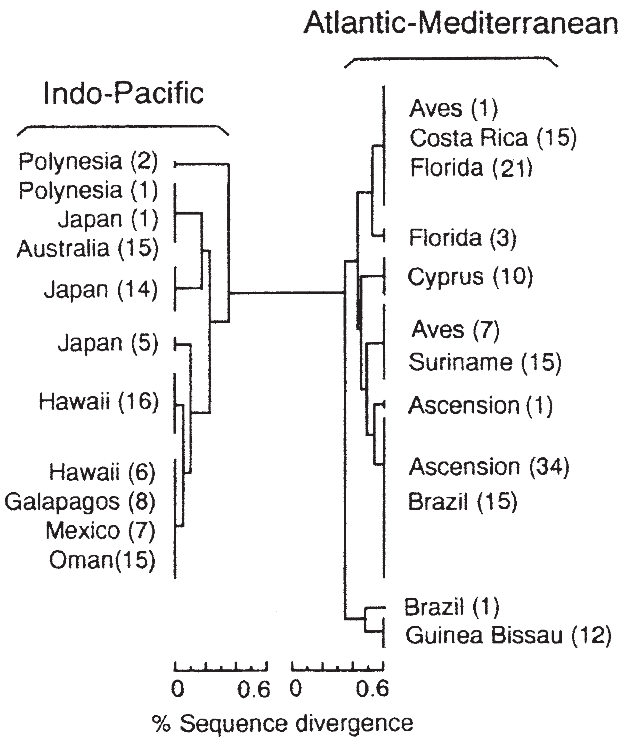

Figure 1. Evolutionarily significant units (ESUs) in the green turtle *Chelonia mydas*. UPGMA dendogram of mtDNA analysed from 15 rookeries in green turtles (study by Bowen *et al.* 1992). A major phylogeographic break is evident between the Indo-pacific and Atlantic Ocean, indicating two separate ESUs, within which are multiple management units. Figure reproduced from Moritz (1994), with permission from Elsevier. Numbers in brackets indicate sample sizes (number of nests).

things, conservation of the gene pool. The concept of evolutionarily significant units (ESUs) helps us to recognize the genetic component of biodiversity and to ensure that the evolutionary heritage of a species is recognised and conserved, thus setting priorities for conservation (Moritz 1994). ESUs define historical population structure to reveal divisions in species that reflect their evolutionary past. Whilst this indicates past isolation, and therefore we cannot predict future outcomes from it, it does indicate where lineages within a species have been actively dividing and thus where evolutionary potential may be found. Genetic data from the endangered green turtle *Chelonia mydas* have suggested two separate ESUs, with a major phylogenetic break occurring between the Atlantic and Indo-Pacific groups. Each unit should be managed separately to maintain this evolutionary heritage (Figure 1; Bowen *et al.* 1992).

Other examples come from: medicine, such as understanding the evolution of drug resistance in HIV (Freeman & Herron 2007); agriculture, such as evolution of pesticide resistance in insect pests (Taylor 1986); fisheries management, such as size-selective fishing causing evolution of fish populations (Conover & Munch 2002); and human behavioural evolution, such as human perceptions of attractiveness (Peters *et al.* 2007). There are many other examples from which teachers can choose to tailor applications to their students' interests and field of study. Such examples can also help to show the relevance of evolution to socio-scientific issues (Bizzo & El-Hani 2009).

What should we teach?

Teachers of evolution are inevitably confronted with the difficult question of selecting which aspects of evolution to teach in introductory and specialist biology units. We argue that the difference between the introductory and the specialist units is one of breadth rather than depth, so the major themes of evolution should be at least touched on for beginning students. We also argue that all material should be presented in the context of scientific method, so that science is understood as a process rather than a body of knowledge to be memorised, and that practical examples should be used wherever possible of the topic's relevance to contemporary life. Content might vary depending on the course-context in which evolution is taught, but there are some basic principles that should be covered and can be found in the chapter headings of any good evolutionary text.

Evidence for evolution

First and foremost should be a clear understanding of the evidence for evolution. A range of evidence from different disciplines and on different scales can show that (i) populations within species show evolutionary change in heritable traits (population studies of microevolution, breeding of domesticated plants and animals), (ii) this within-species change can lead to the evolution of new species (biogeography of ring species, transitional forms in the fossil record, genetics of polyploidy in plants), (iii) all life on earth shares a common ancestry (lineages within the fossil record, comparative anatomy and embryology, molecular biology and genetics, vestigial traits in morphology, development and genetics). This material can be made contemporary and exciting by including recent examples of all these characteristics (see Coyne 2009, especially chapters 2 and 3). The text books by Freeman & Herron (2007) and Ridley (2004) present insightful and scientifically rigorous chapters reviewing the evidence for evolution, and see Irwin (2001) for a review of ring species.

Microevolution – small scale changes in gene frequencies within populations

Students should also gain a clear understanding of microevolution, its four contributing processes (natural selection, mutation, gene flow and genetic drift) and how they contribute to gene frequency change in populations. There are good Australian examples of microevolution. One is the response of snake species to the introduction of the cane toad *Bufo marinus* to Australia. The cane toad was introduced in 1935 to control insect pests, principally of the cane beetle, but was ineffective in its primary role. Nevertheless, it thrived under Australian conditions and spread from its original introduction sites in Queensland across much of northern Australia. While native snakes prey on the cane toads, far from controlling toad numbers snakes were often killed by the toad's venom. Snakes with large heads relative to their body size can eat larger toads and therefore ingest more venom. However, if the snake is heavy it can tolerate more venom. Recent studies of two snake species vulnerable to poisoning by cane toads, show that both species have evolved smaller heads and heavier bodies (Phillips & Shine 2004).

Other examples of microevolution include: the evolution of beak shape in Galápogos finches (see Peter and Rosemary Grant and colleagues, Freeman & Herron 2007); adaptive divergence in body size in sockeye salmon (Hendry 2001); evolution of life-history traits in guppies (Reznick *et al.* 1997); and the evolution of beak length in soapberry bugs (Carroll & Boyd 1992; Carroll *et al.* 1997; Carroll *et al.* 2001; Carroll *et al.* 2005; for an overview see Freeman & Herron 2007). All these examples are particularly useful as sound examples of microevolution, because rather than just illustrating phenotypic change, they have also explicitly tested the criterion that the traits involved are genetically based and therefore heritable: a key component of the microevolutionary process.

Studies of natural selection can be used to test each of Darwin's four postulates about populations that inevitably lead to natural selection (Darwin 1859). Darwin's four postulates, which Freeman & Herron (2007) illustrate with examples of snapdragons and Galápogos finches, are:

(i) Individuals within populations are variable

(ii) The variations among individuals are, at least in part, passed from parents to offspring

(iii) In every generation, some individuals are more successful at surviving and reproducing than others, and

(iv) The survival and reproduction of individuals are not random: instead they are tied to the variation among individuals. The individuals with the most favourable variations, those who are better at surviving and reproducing, are naturally selected.

As a consequence, individuals with characteristics well-suited to their environment increase in the population (Freeman & Herron 2007).

Speciation

Integral to understanding evolution is the study of how speciation occurs. Students should appreciate how species are defined, and the difficulties of reaching a consensus species concept. Different modes of speciation should also be explored, including how speciation may occur in space (such as allopatric or sympatric speciation), and what mechanism/s might be involved (such as natural selection, genetic drift, sexual selection or more sudden karotypic changes) (Freeman & Herron 2007).

Macroevolution – large scale change beyond speciation

The final essential component in general undergraduate studies of evolution is an understanding of the difference between microevolution and macroevolution, and an appreciation of macroevolutionary patterns. Students should gain an overview of the history of life on earth, an appreciation of the fossil record and how it contributes to our understanding of the relationships of organisms, as well as our understanding of patterns and processes (*sensu* McNamara 2009), and an overview of patterns of extinction and radiation. It is impossible to gain a detailed understanding of the fossil record and how it can be studied in a general evolutionary unit, however, some key topics can be studied in detail to gain the depth of thinking required from advanced students. During detailed reading about the evolution of Cambrian fossil fauna, for example, students can encounter both fossil and molecular evidence which contributes to scientific understanding of whether this truly was an 'explosive' evolutionary event (Mapstone & Mapstone 2003; Peterson *et al.* 2005). Students can then be encouraged to critically evaluate what these two disciplines tell us about how and when the Cambrian fauna evolved. They can also integrate their ecological knowledge when they encounter discussions on the role of ecological triggers in Cambrian evolution.

New directions in evolutionary research

Evolution for advanced students should not just stay on steady ground, but should also explore the frontiers of evolutionary science. Students should be readily aware that there are many questions still unanswered, with differing viewpoints and models currently being tested (McBride *et al.* 2009). Delving into some of these issues, for example the importance of genetic drift versus natural selection in driving molecular evolution (see Freeman & Herron 2007 for an overview), provides insight into how research can be used to evaluate different hypotheses, and provides another stimulus for critical thinking.

How should we teach it?

Here we explore specific case studies in more detail to illustrate the teaching elements within them, and thus show how evolution can be taught as inquiry learning, in which students focus on the process of science rather than learning content by rote (Finn *et al.* 2002).

Evolution as a stimulus for teaching critical thinking skills

Developing critical thinking and analysis skills should be central in teaching evolution. In particular, advanced undergraduates can synthesize their learning to solve problems, thereby developing their analytical thinking skills.

The availability of information by electronic sources means that the role of the university teacher has shifted somewhat from disseminating information, to facilitating access to the *most accurate, useful and relevant* types of information. It is useful for students to reflect on just how accurate some of the 'fast information' they access might be. One way to stimulate critical reflection is to have students read an online news article from a mainstream news outlet which reports on the findings of evolutionary research. The article could be reporting on bacterial conjugation, human evolution, population genetics or any topic with an evolutionary slant (see Table 1 for a listing of useful online news sites). Students should read with a critical eye, looking at whether there are significant compromises in how the scientific principles are explained for a mainstream audience. The students' job is then to find the published research article on which the news story is based (using clues given in the news story, such as authors and date). They should also read around the topic to gain a deeper understanding of the original research before writing a

Table 1

Examples of news websites and popular magazine sites that publish stories reporting on research in science. The stories on these sites focus on particular research studies and are just some of the sites that are useful sources of evolution stories for undergraduate students to research and critique.

Website	URL
Science Daily	http://www.sciencedaily.com/news/ http://www.sciencedaily.com/news/plants_animals/biology/
BBC News (Science and Environment)	http://news.bbc.co.uk/2/hi/science/nature/default.stm
ABC News (Environment and Nature)	http://www.abc.net.au/science/news/default.htm?site=science&page=01&topic=enviro
New Scientist	http://www.newscientist.com/
Cosmos	http://www.cosmosmagazine.com/

critique examining how accurately and effectively the news story reports the research from the scientific paper. It can help for students to have small-group discussions, facilitated by the tutor/lecturer, where they examine the research and any oversimplifications made in the news story, and explore some of the reasons why those oversimplifications might be there. Through the critique process they should gain an understanding of just how superficial scientific information is when it comes from these 'fast' sources. There is no substitute for finding the original research and reading it critically.

The Honey Possum – a showcase for developing hypotheses and testing them with structured observations

Sex is a sure subject for sparking interest amongst undergraduate students as well as being a highly relevant topic to explore from the perspective of evolution. One sexual athlete worthy of attention is the Australian honey possum *Tarsipes rostratus*. Honey possums are endemic to the south-west corner of Western Australia, and feed exclusively on nectar and pollen (Wooller *et al.* 1984; Wooller *et al.* 2004). Although tiny and weighing 6–9 g, males of this species produce the longest sperm recorded for any mammal (Cummins & Woodall 1985). Their testes represent approximately 4.2% of their total body weight (Renfree *et al.* 1984), making them much larger than those of any other marsupial, most of whom have a relative testes mass of less than 1% (Taggart *et al.* 1998), and amongst the largest recorded for eutherian mammals (Kenagy & Trombulak 1986; Breed & Taylor 2000).

In our own teaching, the honey possum example becomes a case study in sexual selection. Sexual selection arises due to asymmetries in reproductive success within and between the sexes (Freeman & Herron 2007). One form of sexual selection is sperm competition, which occurs as a consequence of female multiple mating, where the gametes of two or more males compete to fertilize a given set of ova (Birkhead & Møller 1998; Parker 1998; Anderson & Dixon 2002). Before using this example students should be familiar with the basics of sperm competition and the characteristics it selects for in males. Extensive research has found that in species where females mate with more than one male in a single reproductive event (multiple mating), the relative testes mass is greater than in species where females mate with a single male (Gomendio *et al.* 1998). Larger testes indicate a larger investment in spermatogenesis (Harvey & Harcourt 1984; Møller 1988; 1989). This observation is seen across a range of taxa including primates, ungulates, other eutherian mammals, marsupials, birds, fish, frogs, and butterflies (Birkhead & Møller 1998, chapters and references therein). This *observational* evidence is tested by *experimental evolution* in the laboratory, where testes mass has been shown to increase in response to polyandrous mating (*e.g.*, see Hosken & Ward 2001). It is further used to *predict* the direction of evolution, as in feathertail gliders, where testes mass was used to predict sperm competition (Taggart *et al.* 1998); a fact later confirmed using genetic studies (Parrot *et al.* 2002).

Thus, using this research as a springboard, the large relative testes size in the honey possum (but not necessarily sperm length, see: Gomendio & Roldan 1991; Gomendio *et al.* 1998; Gage & Freckleton 2003) predicts that this species has sperm competition and multiple mating. In addition the students will also discover that there are other intriguing features about the honey possum that indicate sexual selection, such as a strong skew in the operational sex ratio (*sensu* Emlen & Oring 1977; Reynolds 1996). At any one time more males than females are ready to breed because males can produce sperm in all months, while females in the population are asynchronous in their timing of oestrus, due to continuous year-round breeding, embryonic diapause and a brief oestrus duration (Bryant 2004). This creates competition amongst males: another flag to students that sexual selection is at work.

The case study can be further developed by exploring the genetic research on whether there is sperm competition in the honey possum. Female honey possums and the 2–4 pouch-young they were carrying, were genotyped at four highly polymorphic microsatellite loci using fluorescently labelled DNA primers (Bryant 2004; Bryant unpublished data). Offspring genotypes were compared to the maternal genotype, and paternal alleles were identified (see Figure 2) to distinguish multiply sired litters (multiple paternity). In all mammals, all ova are released simultaneously, thus multiple paternity provides unquestionable evidence of sperm competition (Gomendio *et al.* 1998).

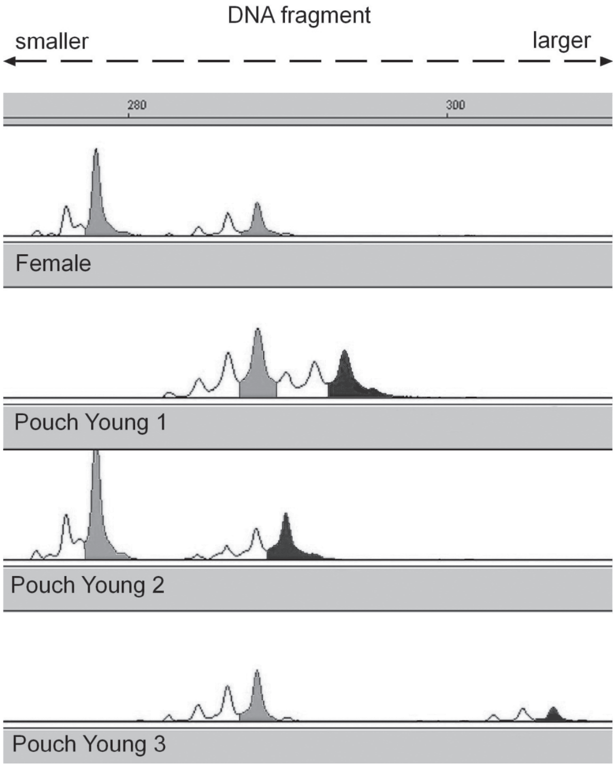

Figure 2. Example of parental allelic identification for a litter of pouch-young at one microsatellite locus for the honey possum *Tarsipes rostratus* (data from Bryant 2004). Microsatellite loci are genotyped for each individual using fluorescently labelled DNA primers, and different alleles are separated by size. Each allele for a dinucleotide locus (pictured here) consists of a primary peak followed by several stutter peaks. Each pouch-young has one maternally derived allele (shown in grey), thus allowing identification of paternal alleles (shown in black). A multiply sired litter is evident where, as in this case, there are ≥ 3 different paternal alleles.

These genetic methods confirmed sperm competition in the honey possum, with multiple paternity in 86% litters (n=35), using a minimum number of sires per litter method, and in 95% litters (n = 41), using an estimated number of sires method based upon the relatedness of litter mates (Bryant 2004; Bryant unpublished data). This indicates that multiple mating is frequent in female honey possums, provides evidence for a high risk of sperm competition amongst males, and confirms sexual selection in a species which has a large investment in sperm production.

The honey possum is therefore an excellent example for inquiry learning about sexual selection, because students must approach the issues using scientific method. They begin with observations, proceed to predictions and then see how those predictions are tested through careful collection of observational data. Using examples of research in teaching makes evolutionary investigation accessible to students, who might otherwise only read about the high profile research highlights in text books, magazines and international journals. It demonstrates that sound discoveries in evolution can be made on a local scale. Local examples, provide interest and evidence that evolution is a dynamic process, not only observed over geological timescales, but also happening in the bush just outside one's backdoor. We have also found that our own students respond well to hearing what their own faculty are researching. However, other case studies could be substituted here with the same effect, exploiting students' inherent interest in 'home industry'.

Trinidad guppies – developing hypotheses and testing them with manipulative experiments

The next example, the Trinidadian Guppy, is also studied following scientific methods. Once again, students begin with an observation and make a prediction, but in this case the prediction is put to an experimental test. Thus, this example illustrates good principles of experimentation in illustrating evolutionary phenomena.

The Trinidad Guppy *Poecilia reticulata* is a wild freshwater fish found in mountain streams in the tropical forests of north-eastern South America and adjacent islands (Endler 1980). Generally, guppies living under high predation conditions are found downstream of waterfalls, together with the pike cichlid *Crenichichla alta* and other species of cichlids that prey on large, mature guppies (Reznick *et al.* 1997). Guppies living under low predation conditions are found upstream where large predators cannot traverse up waterfalls or rapids. In these populations guppies are found with *Rivulus hartii*, an omnivore that sometimes preys on juvenile guppies.

Endler's (1980) classic experiments on the guppies investigated natural selection on the colouration patterns (bright spots and patches of colour) found on adult male guppies. The colour genes are not expressed in females. Endler (1980) hypothesized that males in streams with cichlid fishes had fewer spots due to selection pressure from predation, and he tested this in two ways. Firstly, he created a mixed guppy population from a variety of streams, divided these fish randomly amongst artificial ponds, and to each pond added either a cichlid fish, *Rivulus*, or no other fish. Over 19 months the guppies in the control ponds and *Rivulus* ponds exhibited an increase in the average number of spots due to sexual selection, whereas the guppies in the cichlid ponds exhibited a decrease in the average number of spots associated with predation (Endler 1980). Secondly, Endler tested this effect in the wild in the Aripo river in Trinidad. He translocated guppies from a stream where they were living with cichlids, to a stream with *Rivulus* but no guppies, and compared them to a control stream where guppies were already living with *Rivulus*. After about two years, the average number of spots in the translocated guppy population had increased to become similar to the *Rivulus*-only guppies, diverging from the lower number of spots found in the cichlid-stream guppies.

Evobeaker® (Simbio Virtual Labs 2010) provides a computer simulation 'How the guppy got its spots' (SimBio Virtual Labs 2009) which allows students to investigate guppy spot brightness first hand, rather than just reading about the Endler experiments. It is useful if students are not exposed to the Endler experiments until after they have done at least some initial hypothesis building and experimentation of their own. Using Evobeaker® software, students can design and carry out experiments to test their hypotheses in a complex environment with a range of streams, artificial ponds and predators. Under the simulation, spot brightness decreases under predation from cichlids, in comparison to controls, similar to the findings of Endler's (1980) experiments. There are opportunities for the more advanced and motivated students to refine their experimentation, after a few initial experiments, and include testing, for example, for the impact of different types of cichlids, different abundances of cichlids, the impact of *Rivulus*, and the impact of different stream environments, and to record the observation that spot brightness increases when predation pressure is released (due in the wild to sexual selection, Endler 1980). This allows depth in the learning of both the process of natural selection and the research skills needed to study it. The approach used in the guppy exercise is constructivist: where a problem is proposed, alternatives are put forward, and evidence is gathered to address the problem, and this type of approach is thought to increase learning and retention (Alters & Nelson 2002).

The guppy work also provides linkages to learning about life history evolution. Reznick and co-workers (1987; 1990; 1997) have investigated predation pressure as a driver of life history evolution by performing translocation experiments. The work started with observations by these workers and others (Reznick *et al.* 1997 and references therein) that guppies from high predation populations have a higher mortality rate and 'faster' life history strategy than guppies from low predation populations (Reznick & Endler 1982; Reznick *et al.* 1997). They mature earlier, at a smaller size, and they reproduce more frequently, with each litter containing more young of a smaller size than low-predation guppies, as predicted under life-history theory (Reznick & Endler 1982). These differences have a genetic basis (Reznick 1982).

The descendants of guppies that were translocated from high to low predation, matured at a later age and larger size than those in the control population under high predation (Table 2), and produced fewer, larger offspring (Reznick & Bryga 1987; Reznick *et al.* 1990; Reznick *et al.* 1997). This response was measured after 11 years in the Aripo River and at both 4 and 7.5 years in the El Cedro River, with a slower response in the female traits than in the male traits, likely due to a lower heritability (Reznick *et al.* 1997). Thus the differences in life history traits observed in high and low predation populations of guppies were shown through experimental evidence to be a consequence of these high and low predation environments. The primary selection force is thought to be predation, along with a role from selection based on differences in resource availability in high and low predation communities (see Reznick *et al.* 2001).

The research undertaken in this case study exemplifies how observations can be taken through to experimentation to test the actual drivers of natural selection on gene frequencies in populations, and how they have shaped life histories in the past. Students can also reflect on experimental design, especially the use of controls, to develop their critical thinking skills (Alters & Nelson 2002). It also provides a clear example of natural selection occurring rapidly over ecological timescales (albeit through selection imposed by experimental means), dispelling the misconceptions that evolution *only* happens extremely slowly over geological timescales (which probably arises due to problems with use of the term 'gradual' in descriptions of natural selection; it can refer purely to the *process* as being incremental rather than the *rate* being constant; see Ridley 2004, box 21.1), and that only events at the speciation level and above count as true evolution (for a student-friendly article see Holmes 2005). Addressing student misconceptions is a key part of the learning process (Alters & Nelson 2002). Finally, for advanced students, this example can be used in discussions about the processes of micro- versus macroevolution. Reznick *et al*. (1997) use this example to show that selection among individuals within populations can occur rapidly enough to account for the periods of rapid change observed in the fossil record, and thus contribute to the debate on whether the pattern of punctuated equilibrium must be explained using different processes to those of microevolution (see also Svensson 1997).

Table 2

Measurements of male and female age and size at maturity for low predation (experimental) sites and high-predation (control) sites of guppies *Poecilia reticulata* in a translocation experiment by Reznick *et al.* (1997). These are measurements from second generation laboratory-reared descendents of the guppies from the wild populations. Measurements are least squares means adjusted for covariates and unequal samples sizes and * indicates statistical significance (see details in Reznick *et al.* 1997).

Measurement (at maturity)	Control (high predation)	Experimental (low predation)
Aripo river (11 years/18.1 generations)		
Male age (days)	48.6	58.2*
Male size (mg)	67.5	76.1*
Female age (days)	85.6	93.5*
Female size (mg)	162.3	189.2*
El Cedro River (4 years/6.9 generations)		
Male age (days)	60.6	72.7*
Male size (mg)	56.0	62.4*
Female age (days)	94.1	95.5
Female size (mg)	116.5	118.9
El Cedro River (7.5 years/12.7 generations)		
Male age (days)	47.3	52.5
Male size (mg)	71.5	74.4*
Female age (days)	75.8	80.4
Female size (mg)	141.8	152.1*

Data from Reznick *et al.* 1997

Student background: an important issue

In choosing examples to be presented, it is important to be aware of students' backgrounds. For example, many topics in evolution can be explored using sophisticated mathematical models. We have presented none of these, because in our experience many students lack the mathematical background necessary to fully appreciate these examples. However, instructors whose students are not restricted in this way may prefer to develop some of the mathematical approaches. This could include, for example, statistical analyses of the results of experiments (Ruxton & Colegrave 2006) or introductions to mathematical modelling (Calver & Wooller 1998), and a detailed treatment of quantitative concepts in population genetics (Ridley 2004).

Instructors need to assess the cultural appropriateness of examples too. Many hereditary human diseases are interesting teaching examples, but some students may be particularly sensitive about these matters. Similarly, while our honey possum example is interesting to our Australian students, we can well imagine why it would be an inappropriate example in other cultural contexts.

Religious perspectives and beliefs are a sensitive issue. We are not advocating discussion of creation science or intelligent design alongside evolution, but some students come to classes prejudiced against evolution (Chinsamy & Plagányi 2008; Sanders & Ngxola 2009) and we agree with Slingsby (2009) that these prejudices should be treated with 'philosophical neutrality'. Anticipating these views is as much a part of preparation as mastering the subject matter or dealing with students' poor backgrounds in mathematics or English. Excellent suggestions on responding to students fearful or hostile to studying evolution are discussed with sensitivity from a range of cultural perspectives in Jones & Reiss (2007). Instructors may also find value in Dobzhansky (1973), who argues the compatibility of evolution and religion.

After the classroom

We would hope that students introduced to some of the processes and ideas that we described above will appreciate that evolution does not simply equal speciation. Rather, we hope that they will understand that it is a dynamic process occurring at generational as well as geological timescales. Using examples in teaching that can contribute to a range of areas in evolutionary thinking, helps to encourage synthetic and critical thinking in our students. They should also have a clearer idea of scientific evidence and scientific process, especially developing predictions from hypotheses and submitting these predictions to observational and experimental tests. Students should be able to apply their critical thinking, powers of synthesis and logic not only to evolutionary problems, but to other issues that they encounter in all areas of life.

References

Alters B & Nelson C 2002 Perspective: teaching evolution in higher education. Evolution 56: 1891–1901.

Anderson M J & Dixon A F 2002 Motility and the midpiece in primates. Nature 416: 496.

Barker J A 1983 The giant nematode 'Nematodius' spp. Journal of Biological Education 17: 199–200.

Birkhead T R & Møller A (eds) 1998 Sperm Competition and Sexual Selection. Academic Press, London.

Bizzo N & El-Hani C 2009 Darwin and Mendel: evolution and genetics. Journal of Biological Education 43: 108–114.

Bleckmann C A 2006 Evolution and creationism in science: 1880–2000. Bioscience 52: 151–158.

Bowen B W, Meylan A B, Ross J P, Limpus C J, Balazs G H & Avise J C 1992 Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. Evolution 46: 865–881.

Breed W G & Taylor J 2000 Body mass, testes mass, and sperm size in murine rodents. Journal of Mammalogy 81: 758–768.

Bryant K A 2004 The mating system and reproduction in the honey possum, *Tarsipes rostratus*: a life-history and genetical perspective. PhD Thesis, Murdoch University, Perth.

Calver M C & Wooller R D 1998 A non-destructive laboratory exercise for teaching some principles of predation. Journal of Biological Education 33: 45–48.

Carroll S & Boyd C 1992 Host race radiation in the soapberry bug: natural history with the history. Evolution 46: 1052–1069.

Carroll S, Dingle H, Famula T & Fox C 2001 Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, *Jadera haematoloma*. Genetica 112–113: 257–272.

Carroll S, Dingle H & Klassen S 1997 Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. Evolution 51: 1182–1188.

Carroll S, Loye J, Dingle H, Mathieson M, Famula T & Zalucki M 2005 And the beak shall inherit – evolution in response to invasion. Ecology Letters 51: 944–951.

Chinsamy A & Plagányi E 2008 Accepting evolution. Evolution 62: 248–254.

Conover D O & Munch S B 2002 Sustaining fisheries yields over evolutionary timescales. Science 297: 94–96.

Coyne J 2009 Why evolution is true. Oxford University Press, Oxford.

Cummins J M & Woodall P F 1985 On mammalian sperm dimensions. Journal of Reproduction and Fertility 75: 153–175.

Darwin C 1859 On the origin of species by means of natural selection. Murray, London.

Dobzhansky T 1973 Nothing in biology makes sense except in the light of evolution. The American Biology Teacher 35: 125–129.

Emlen S T & Oring L W 1977 Ecology, sexual selection, and the evolution of mating systems. Science 197: 215–223.

Endicott P, Ho S Y W, Metspalu M & Stringer C 2009 Evaluating the mitochondrial timescale of human evolution. Trends in Ecology and Evolution 24: 515–521.

Endler J 1980 Natural selection on color patterns in *Poecilia reticulata*. Evolution 34: 76–91.

Finn H, Maxwell M & Calver M 2002 Why does experimentation matter in teaching ecology? Journal of Biological Education 36: 158–162.

Freeman S & Herron J C 2007 Evolutionary Analysis. Pearson Prentice Hall, Upper Saddle River NJ.

Gage M J G & Freckleton R P 2003 Relative testis size and sperm morphometry across mammals: no evidence for an association between sperm competition and sperm length. Proceedings of the Royal Society of London, Series B 270: 625–632.

Gendron R P & Staddon J E R 1984 A laboratory simulation of foraging behavior: the effect of search rate on the probability of detecting prey. American Naturalist 124: 407–415.

Gomendio M, Harcourt A H & Roldán E R S 1998 Sperm competition in mammals. *In*: T R Birkhead & A P Møller (eds), Sperm Competition and Sexual Selection. Academic Press, London, 667–755.

Gomendio M & Roldan E R S 1991 Sperm competition influences sperm size in mammals. Proceedings of the Royal Society of London, Series B 243: 181–185.

Groom M J, Meffe G K & Carroll C R 2006 Principles of conservation biology. Sinauer Associates, Inc., Sunderland, Massachusetts.

Gwynne D T 1981 Sexual difference theory: Mormon crickets show role reversal in mate choice. Science 213: 779–780.

Harvey P H & Harcourt A H 1984 Sperm competition, testes size, and breeding systems in primates. *In*: R L Smith (ed), Sperm Competition and the Evolution of Animal Mating Systems. Academic Press, Florida, 589–600.

Hendry A P 2001 Adaptive divergence and the evolution of reproductive isolation in the wild: an empirical demonstration using introduced sockeye salmon. Genetica 112–113: 515–534.

Holmes B 2005 In the blink of an eye. New Scientist 9 July 2005: 28–31.

Hosken D J & Ward P I 2001 Experimental evidence for testis size evolution via sperm competition. Ecology Letters 4: 10–13.

Irwin D, Irwin J & Price T 2001 Ring species as bridges between microevolution and speciation. Genetics 112–113: 223–243.

Jones L & Reiss M 2007 Teaching about scientific origins: taking account of creationism. Peter Lang publishing, New York.

Kenagy G J & Trombulak S C 1986 Size and function of mammalian testes in relation to body size. Journal of Mammalogy 67: 1–22.

Kettlewell H 1973 The evolution of melanism. Oxford University Press, Oxford.

Mapstone B & Mapstone G 2003 The Burgess Shale hike: evolution in a day. The Linnean 19: 24–41.

McBride P, Gillman L & Wright S 2009 Current debates on the origin of species. Journal of Biological Education 43: 104–107.

McNamara K 2009 The importance of developmental repatterning in the evolution of trilobites. Journal of the Royal Society of Western Australia (This volume).

Møller A P 1988 Ejaculate quality, testes size and sperm competition in primates. Journal of Human Evolution 17: 479–488.

Møller A P 1989 Ejaculate quality, testes size and sperm production in mammals. Functional Ecology 3: 91–96.

Moritz C 1994 Defining 'evolutionarily significant units' for conservation. Trends in Ecology and Evolution 9: 373–375.

Nardi F, Carapelli A, Dallai R & Frati F 2003 The mitochondrial genome of the olive fly Bactrocera oleae: Two haplotypes from distant geographical locations. Insect Molecular Biology 12: 605–611.

Parker G A 1998 Sperm competition and the evolution of ejaculates: towards a theory base. *In*: T R Birkhead & A P Møller (eds), Sperm Competition and Sexual Selection. Academic Press, London, 3–54.

Parrot M, Ward S & Taggart D 2002 The mating system of the feathertail glider (*Acrobates pygmaeus*): investigation into the likelihood of sperm competition and multiple paternity. 48th Scientific Meeting of the Australian Mammal Society, Warrnambool.

Peters M, Rhodes G & Simmons L W 2007 Contributions of the face and body to overall attractiveness. Animal Behaviour 73: 937–942.

Peterson K J, McPeek M A & Evans D A D 2005 Tempo and mode of early animal evolution: inferences from rocks, Hox, and molecular clocks. Paleobiology 31: 36–55.

Phillips B L & Shine R 2004 Adapting to an invasive species: Toxic cane toads induce morphological change in Australian snakes. Proceedings of the National Academy of Sciences of the United States of America 101: 17150–17155.

Renfree M B, Russell E M & Wooller R D 1984 Reproduction and life history of the honey possum, *Tarsipes rostratus*. *In*: A P Smith & I D Hume (eds), Possums and Gliders. Australian Mammal Society, Sydney, 427–437.

Reynolds J D 1996 Animal breeding systems. Trends in Ecology and Evolution 11: 68–72.

Reznick D 1982 The impact of predation on life history evolution in Trinidadian guppies: genetic basis of observed life history patterns. Evolution 36: 1236–1250.

Reznick D & Bryga H 1987 Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. Evolution 41: 1370–1385.

Reznick D, Butler M & Rodd H 2001 Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. The American Naturalist 157: 126–140.

Reznick D & Endler J A 1982 The impact of predation on life-history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution 36: 160–177.

Reznick D N, Bryga H & Endler J A 1990 Experimentally induced life-history evolution in a natural population. Nature 346: 357–359.

Reznick D N, Shaw F H, Rodd F H & Shaw R G 1997 Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275: 1934–1937.

Ridley M 2004 Evolution. Blackwell Science, Malden, MA.

Ruxton G D & Colegrave N 2006 Experimental design for the life sciences. Oxford University Press, Oxford.

Samways M J 1994 Insect conservation biology. Chapman and Hall, London.

Sanders M & Ngxola N 2009 Identifying teachers' concerns about teaching evolution. Journal of Biological Education 43: 121–128.

SimBio Virtual Labs 2009 How the guppy got its spots. Simbiotic Software for Teaching and Research, Inc, Ithaca, NY.

Simbio Virtual Labs 2010 Evobeaker. Simbiotic Software for Teaching and Research, Inc, http://simbio.com/products-college/EvoBeaker.

Slingsby D 2009 Charles Darwin, biological education and diversity: past present and future. Journal of Biological Education 43: 99–100.

Svensson E 1997 The speed of life-history evolution. Trends in Ecology and Evolution 12: 380–381.

Taggart D A, Breed W G, Temple-Smith P D, Purvis A & Shimmin G 1998 Reproduction, mating strategies and sperm competition in marsupials and monotremes. *In*: T R Birkhead and A P Møller (eds), Sperm Competition and Sexual Selection. Academic Press, San Diego, 623–666.

Tarlinton R E, Meers J & Young P R 2006 Retroviral invasion of the koala genome. Nature 442: 79–81.

Taylor C 1986 Genetics and evolution of resistance to insecticides. Biological Journal of the Linnean Society 27: 103–112.

Wilson E 1998 Consilience. Vintage Books (a division of Random House), New York.

Wooller R, Richardson K, Saffer V, Garavanta C, Bryant K, Everaardt A & Wooller S 2004 The honey possum *Tarsipes rostratus*: an update. *In*: R Goldingay & S Jackson (eds), The biology of Australian possums and gliding possums. Surrey Beatty & Sons, Chipping Norton.

Wooller R D, Russell E M & Renfree M B 1984 Honey possums and their foodplants. *In*: A P Smith and I D Hume (eds), Possums and Gliders. Australian Mammal Society, Sydney, 439–443.