

Come to Me, My Melancholic Baby!

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Some famous textbook cases of evolution aren't unambiguously true. Does it matter?

There's not much point in writing a column about things we already know, but there is value in looking at things we *thought* we already knew. One way to do this is to see how textbooks illustrate basic principles. I was led to write this column when my daughter took an introductory bioanthropology course this year and asked me something about natural selection. Her class had been discussing the example of industrial melanism and the peppered moth. I found that curious, because I thought I had seen several years ago that that example had been undermined by contradictory evidence from color changes in the same moths in North America. How could it still be in textbooks?

This brought to mind Stephen Jay Gould's making fun in *Natural History* of the classic description of the early horse *Eohippus* (or *Hyracotherium*) as being the size of a fox terrier (Figure 1). This comparison was first used in 1904 by the paleontologist H. F. Osborn in reconstructing horse evolution. The simile was then copied from textbook to textbook by authors—and for readers—who, like me, probably had little idea even what a fox terrier looked like. And according to Gould,

the comparison was wrong. He said the horse was bigger. Of course, we have to presume that he himself had actually *seen* a fox terrier.

As so often happens, something similar came up coincidentally in an unrelated conversation, and is closer to anthropology. In 1940 the prominent geneticist A. H. Sturtevant suggested that tongue-rolling ability illustrated the genetic control of human traits, and we've used it as a classroom example ever since (are you TT or tt?). It costs nothing to test in students, and if you assume a dominant gene in Hardy-Weinberg equilibrium you can always estimate the allele frequency. However, in 1965 Sturtevant retracted his suggestion that the trait was genetic, saying "I am still embarrassed to see it listed in some current works as an established Mendelian case." Tongue rolling has still not been completely displaced as a classroom example of Mendelian inheritance, but if it is genetic at all, it's neither a simple single-locus trait nor even a single biological trait, and may in fact be something most people can acquire during a critical developmental period.

These whimsical examples of textbook echoing illustrate Lewis Carroll's promise in *The Hunting of the Snark* that "what I tell you three times is true." But this may not always be trivial, so it is worth looking at cases in which questions have been raised about the two classic examples used to buttress core concepts of evolutionary biology, which could have serious practical consequences if the examples are wrong.

CATCHING EVOLUTION IN THE ACT

Of Birds and Bugs

*Come to me, my melancholy baby,
Cuddle up and like your hue . . .
All your fears are foolish fancy,
maybe
You know dear, that I'll be true to
you.*

*Every smog may have a silver lining,
But until the sun shines through,
Smile, my honey dear,
While I kiss away each tear,
'Cause I'll be staying melancholic
too!*

A quick check of the web confirmed my recollection that numerous problems had been raised about industrial melanism as an example of natural selection observed in action (and touted by creationists as disproving the evolutionary edifice) (see Majerus and B. S. Grant references). What are these issues?

In 1896 J. W. Tutt suggested protective coloration against bird predation as an explanation of the rapid recent rise in the frequency of melanic forms of the peppered moth *Biston betularia* in Britain. The selective force was predation facilitated by industrial air pollution. Most moths had been of the light-colored *typica* form with black speckles, and enjoyed protective coloration on lichen-covered trees where they were hard for birds to see, because they dramatically resemble the mottled pattern of lichens (Figure 2). But soot from the industrial revolution blackened the trees in the 19th century, killed the lichens, and deprived the moths of their protective

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Figure 1. Horse and Hounds? (Not to scale.) Courtesy www.nature.ca/nature_e.cfm and www.akc.org.

cover. This favored a formerly rare melanic variant whose peppering black spots were so large that the wings were essentially all black, conferring reversed protective coloration against the newly blackened trees. The *carbonaria* form rose rapidly in frequency. As pollution waned after Clean Air Acts were passed in the 20th century, the variant frequencies reverted towards the lighter peppered form.

This selective hypothesis was examined theoretically by the leading population geneticist J. B. S. Haldane and others in the 1920s. In the 1950s Bernard Kettlewell undertook a series of famous experiments to demonstrate it directly. Among other tests, he placed moths on trees and observed cryptic to non-cryptic predation rates by birds. This became, and remains, the classic *direct* demonstration of evolution by natural selection. However, many aspects of this work have been questioned. I mention some of them to illustrate the problems.

To the human eye the moths seemed to enjoy cryptic protection, but evidence suggests that birds can see into the UV light spectrum, which means that protective coloration may be less effective to them than it is to the scientists suggesting the hypothesis. Kettlewell performed his experiments under various artificial conditions. He used unnatural moth densities in his experiments, and he released the moths in daylight, when they quickly landed on the nearest

(and hence most exposed) places on the tree trunks; normally these moths hide in the branches, and are active only at night when birds aren't. Kettlewell stressed the role of lichens because they appeared to provide an exceptionally cryptic background for the peppered form, but there has been debate about whether moths preferentially seek lichens that match their own color, which would obviate predation based on color. Even the correlation of morph frequency with the presence of lichens is imperfect in Britain, so geographic anomalies between pollution and melanic frequency have had to be explained after the fact by invoking gene flow. There

is also evidence of differential mortality in the expected direction, but of *pre*-adult moths, which cannot be attributed to protective coloration. Finally, I was able to confirm my recollection that there was a parallel change in color variants in North American moths, and parallel patterns of industrialization, but lichens were not involved here and the change may be continuing in regions that do not share comparable pollution differences.

It is disturbing that so many aspects of what seemed such a classically simple exemplar of evolution could be credibly questioned. However, it appears that the problems, though serious, do not entirely invalidate the story. If soot and lichens were not involved in the color pattern changes in North America, there *was* a correlation here, as in Britain, with air pollutants like SO_2 that affect reflectance on trees. That's not the same as mimicking lichens, but it is a plausible source of protective coloration. Although several studies showing differential predation by birds of conspicuous moths had various design problems, their findings have been consistently in the expected direction. It is probably true that protective coloration is at most one of several factors that will explain this story. For example, the fact that color changes in two continents have paralleled the history of air pollution is compelling, but we have to beware that we not fall into the common trap of equating correlation with causa-



Figure 2. Liking lichens? Kettlewell's *Biston betularia*. Lichen covered tree with dark and light (lower left) variants. (From Kettlewell, 1956.)

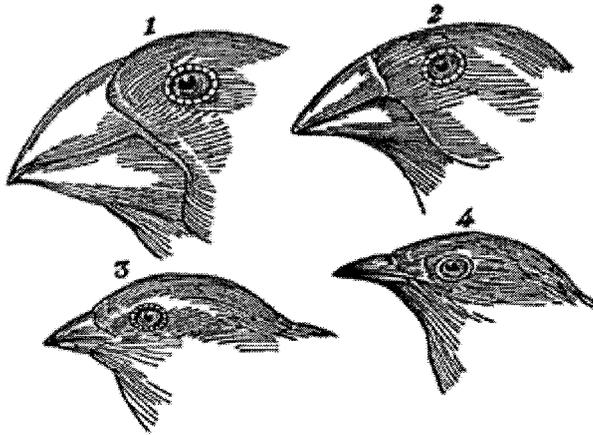


Figure 3. Darwin's finches. (From Darwin's *The Voyage of the Beagle*, 1845.)

tion. Air pollution has been associated with many things, and we may not know them all.

Above all, however, the changes in color frequency have been too rapid, widespread, and consistent to be due to any known factor other than *some* form(s) of natural selection, whether or not we know the exact factors involved. At the very least, the melanism story does illustrate micro-evolution, even if this old chestnut of evolution turns out to be more subtle than the simple textbook tale.

To Speak of Beaks

The oddity of a brief episode of intense selection induced by human industrial pollution may have parallels in more "natural" natural selection. Climate change has also been involved in another classic story, related to the evolution of Darwin's famous Galapagos finches. These birds are so well established as defining instances of adaptive evolution that the Galapagos Islands are on the must see list of biologists the way a hajj to Mecca is in Islam. Everyone knows that after arriving from South America the finches evolved by adaptation to local conditions on the various islands. It is almost mandatory to include this example even in anthropology textbooks. Darwin himself illustrated this adaptive radiation with a drawing of their beak variation (Figure 3). But here, too, the story is not so simple, in interesting ways.

Over the past 30 years, Peter and

Rosemary Grant have observed the Galapagos finches in detail. During this time there have been changes in climate, including droughts that affect plant survival and hence the distribution of available seed sizes. The Grants systematically collected data on survival and census counts of two species (*Geospiza fortis*, medium ground finch; and *Geospiza scandens*, cactus finch). They recently summarized the changes of body size, beak size, and beak shape they observed over this period (Grant and Grant, 2002). On the micro-evolutionary scale, they provide elegant studies of selection, as defined as statistically significant change in trait frequencies from one generation to the next, directly observed in action.

A major finding was that selection occurred in repeated short bursts. When appropriate circumstances existed, the birds showed the expected favorable relative survival of birds with beak characteristics suited for the seed size distribution that existed in a given year, and this really was "selection" in the evolutionary sense that is, it changed the trait distributions in the next generation. But the direction, magnitude, and consistency of these bursts varied among traits and between the species. Stochastic (statistically nonsignificant) changes also occurred, and traits also changed significantly over this period as a result of hybridization and gene flow. There were reversals in the direction of selection, but they did not restore a population to its initial state at the

time their study began. Strong selection in times of drought also did not exhaust variation, as was shown by the birds' ability to respond when rains returned.

Overall, the phenotype changes or states over these 30 years were not predictable from the changes that could have been observed in a single season or short time span. For example, data from the first 5 years could not have been used in population genetics models to predict the 30-year results. Selection certainly occurs, and if your beak is too small you can't eat big tough seeds and won't do well if there aren't any small seeds around. The Grants' major point was a plea for more long-term observational studies, because typical small, short-term observational studies may be insufficient to understand how evolution is actually working. This is clearly appropriate, but there may be two deeper points. First, the kinds of traits Darwin observed are still bouncing around evolutionarily. How confidently can we infer the past selective forces that got the traits to where they are (temporarily) today? And second, *no* observational study is long relative to the evolutionary time scale, which is often what we want to understand. Would even a 100 year study be enough?

COMPLEXITY BURIED WITHIN SIMPLICITY

The true evolutionary story is more complex than the textbooks depiction of a long, steady convergence to an adaptive peak. To many biologists, it may suffice just to know that selection can be demonstrated in the wild. But it is at best less satisfying to have to invoke constantly and rapidly changing mixes of selective forces. We may be getting at least the main selective factors right, but so many things in evolutionary biology dissolve on close inspection, that I'll be crotchety and ask how we know that the other factors were just nuisances, and that results would have been the same if they weren't there. There are many precedents to give us pause about such an assumption.

Diethard Tautz (2000) has expressed the challenge in a memorable

way. The outcome of selection depends on its strength and duration, and on population size. If these factors have roughly quantitatively comparable impact, which may be the rule more than the exception, evolutionary outcomes are fundamentally probabilistic, which Tautz refers to as a "population genetic uncertainty principle," reminiscent of the Heisenberg principle in physics. This could happen even if selection were strong but irregular or episodic, or involved many competing factors. To infer a selection regime under such conditions would require studies that were themselves on an evolutionary or species wide scale.

Butterflies That Won't Migrate and Genes That Do?

These issues, of course, apply in principle to our need to explain human and primate evolution from a mix of fragmentary fossil data and short-term observation, little if any of it as clear as the situation in moths and finches. But I think that more than just the richness of the real evolutionary story is lost in the uncritical repetition of simplistic textbook examples. The subtleties that actually occur have implications for social policy as can be seen by an example of interest to North American anthropologists because it involves one of our favorite species: maize.

A few years ago it was reported that pollen from genetically modified (GM) corn was dangerous to monarch butterflies (Losey et al., 1999; Hansen-Jesse and Obrycki, 2000). This challenged heavily vested interests, and resulted in several studies to see if the reports were true. Generally, the new studies found little if any ill effects (Gatehouse et al., 2002). The original findings in part reflected the intensified experimental exposures that were applied in order to get a useful result in a reasonable time period. This has been standard practice in testing drugs or food additives in mice fed doses many times larger than any human will normally consume, under

the conservative assumption that harm is harm. That's roughly comparable to extrapolating the results of strong short-term selection in finches, so can we trust the results even of well-done but necessarily short-term *natural*-conditions field experiments? The issue is more than just academic, because transgenic insecticide genes may already have escaped from domestic GM corn to wild maize in Oaxaca, Mexico, as was reported by another study (Chapela and Quist, 2001). Despite some methodological problems (*Nature*, April 11, 2002), the authors maintain that their basic finding is true and it has been confirmed. If so, this will constitute evolution in action, but how can we know whether this is something to be concerned about?

Unfortunately, as I was finishing this column the peppered moth story was made the subject of highly publicized scandal-mongering, with the implication that no evidence remained that industrial melanism was an example of evolution in action (see Grant, 2002). Sadly, this *is* likely to change textbooks, which we can predict will make much of the scandal, and that *that*, too will be repeated from book to book. We can only hope that despite the uncertainties the evidence that this *is* a documented evolutionary story will also proliferate.

It is important to raise all appropriate questions about dogma in science. That in both the cases of beaks and spots it has been shown directly that selection works, and that we've probably identified at least some of the forces, *is* a triumph of evolutionary biology. But we should also smile and not be melancholy that weaknesses have been discovered. Weaknesses are not failures. Digesting the message that evolution even in these classic cases is not so clear after all will lead to deeper understanding of evolution and better applications to situations that may really matter, as the maize example may illustrate.

But rather than always having to fight rearguard actions in evolution-

ary biology, it would be nicer if all we had to worry about were tiny horses or rolled-up tongues.

NOTES

Send any comments on this column to: kmw4@psu.edu. I maintain *Crotchety Comments* on my web page: www.anthro.psu.edu/rsrch/weiss_lab.htm. I thank Anne Buchanan, Sam Sholtis, and John Fleagle for critically reading this manuscript; Bruce Grant for moth help; and Chris Carlson for pointing out the tongue-rolling example.

My Melancholy Baby by E. Burnet, music; G. Norton, lyrics; 1912 (e.g., <http://home.swipnet.se/~w-134536/mel27.htm>).

THINGS TO READ

Many things discussed here can be profitably explored by web searching.

Gatehouse AMR, Ferry N, Raemaekers RJM. 2002. The case of the monarch butterfly: a verdict is returned. *Trends in Genetics* 18: 249–251.

Gould SJ. 1988. The case of the creeping fox terrier clone. *Natural History* 97: 16–24.

Grant BS, Owen DF, Clarke CA, Owen DF. 1996. Parallel rise and fall of melanic peppered moths in America and Britain. *J Heredity* 87: 351–357.

Grant BS. 1999. Fine tuning the peppered moth paradigm. *Evolution* 53: 980–984.

Grant BS, Wiseman LL. 2002. Recent history of melanism in American peppered moths. *J Heredity* 93: 86–90.

Grant BS. 2002. Sour grapes of wrath. *Science* 297: 941–942.

Grant PR, Grant BR. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296: 707–711.

Hansen-Jesse LC, Obrycki JJ. 2000. Field deposition of *Bt* transgenic corn pollen: lethal effects on the monarch butterfly. *Oecologia* 125: 241–248.

Kettlewell HBD. 1956. Further selection experiments on industrial melanism in the *Lepidoptera*. *Heredity* 10: 287–301.

Losey J, Rayer LS, Carter ME. 1999. Transgenic pollen harms monarch larvae. *Nature* 399: 214.

Majerus MEN. 1998. *Melanism-evolution in action*. New York: Oxford University Press.

Quist D, Chapela IH. 2001. Transgenic DNA introgressed into traditional maize landraces in Oaxaca, Mexico. *Nature* 414: 541–543.

Sturtevant AH. 1940. A new inherited character in man. *Proc Natl Acad Sci USA* 26: 100–102.

Sturtevant HA. 1965. *A History of Genetics*. New York: Harper and Row.

Tautz D. 2000. A genetic uncertainty principle. *Trends in Genetics* 16: 475–477.

Tutt JW. 1986. *British Moths*. London: Routledge.