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Doin' What Comes Natur'lly

KENNETH WEISS

Behavior affects evolution in many ways. Organisms are adapted for what they do, but they also do what they are adapted for.

In the hit musical *Annie Get Your Gun,* Annie Oakley was a woman trying to make it in the man's world of exhibition sharpshooting in traveling Wild West shows. Women were supposed to do what they were "meant" to do: baking biscuits and tending the chickens and the kids. Annie chose a different path; she didn't have to *evolve* to do that, she just had to develop a skill for which she already had the potential. Her sexist rival, Frank Butler, did not appreciate her unnatural invasion of the male world.

This Wild West tale is about the tension between them, but can be used as a metaphor for issues that arise when we try to understand adaptation and speciation. An important factor of particular relevance to anthropology is behavior. Alfred Wallace did not think humans could have evolved by natural selection, because he thought our mental capacities would have had to be favored by selection for thousands of generations before they were ever used, like the ability to do math (a polymorphic trait even today, however!). Wallace assumed such abilities must therefore come from a Supreme Force, and in this way he used evolutionary arguments to *deduce* the existence of God. We don't have to agree with his conclusion to note that latent capacity is not the same as prescriptive determination. But then, where and how do genes for such traits come into being? Recent genetic work has thrown new light on what had been largely forgotten ideas on ways that behavior is shaped by, but also shapes, evolution.

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ON MEANS OF EVOLUTIONARY CHANGE

There are many ways to make it through life. The usual assumption is that what members of a species do today is what the environment, via natural selection, screened their ancestors to do. Those who didn't, didn't make it. In this view, animals are rather passive recipients of their fate. But in fact animals proactively interact with and in many ways, demonstrably *create* their environments by responding to conditions they face and seeking conditions they like. They are equipped with extensive sensory, locomotor, and other behavioral equipment—and brains—for the purpose. Responsive behavior is the very definition of what it means to be an animal.

Much of an animal's behavior is learned by experience, and traits acquired in that way are not genetically transmitted. However, the discriminating and intentional nature even of learned behavior can nonetheless affect evolution. Sexual selection is behavior that defines fitness, and was central to Darwin's explanation of human evolution. Sexual selection is sometimes called non-adaptive because mating display traits need not be related to the brutal aspects of survival, but behavior can be an important force in that kind of adaptive evolution, too.

Traits Ahead, Genes Catching Up

Explaining the evolution of complex traits in more than generic terms has always been difficult. Ever since Darwin puzzled over the evolution of eyes, the prevailing idea is that such traits evolve through a series of precursors, favored for some reason in their respective times. Lamarck's idea that internal drive towards some desired end was plausible, if acquired traits were heritable as he asserted, but was opposite to Darwin's notion of natural selection in which the environment mechanically screened already-existing variation. In the late 19th century, the nature of inheritance was far from settled. Selection was accepted by some as a possible evolutionary mechanism, but Darwin's ideas on inheritance were wrong. But so were Lamarck's: although Mendel's work was still on the shelves gathering dust, August Weismann had demonstrated the separation of the germ line from the rest of the body, a deathblow to Lamarckian inheritance.

In 1896, the American psychologist James Mark Baldwin[1] and others (Figure 1) including paleontologist Henry Fairfield Osborn suggested a mechanism that might account for the evolution of complex traits, including behavior itself. Baldwin was one of the first experimental psychologists, and had particular interest in social development and transmission, and the evolutionary basis of psychological traits. What became known as the Baldwin Effect was an alternative that could negotiate between, or even en-

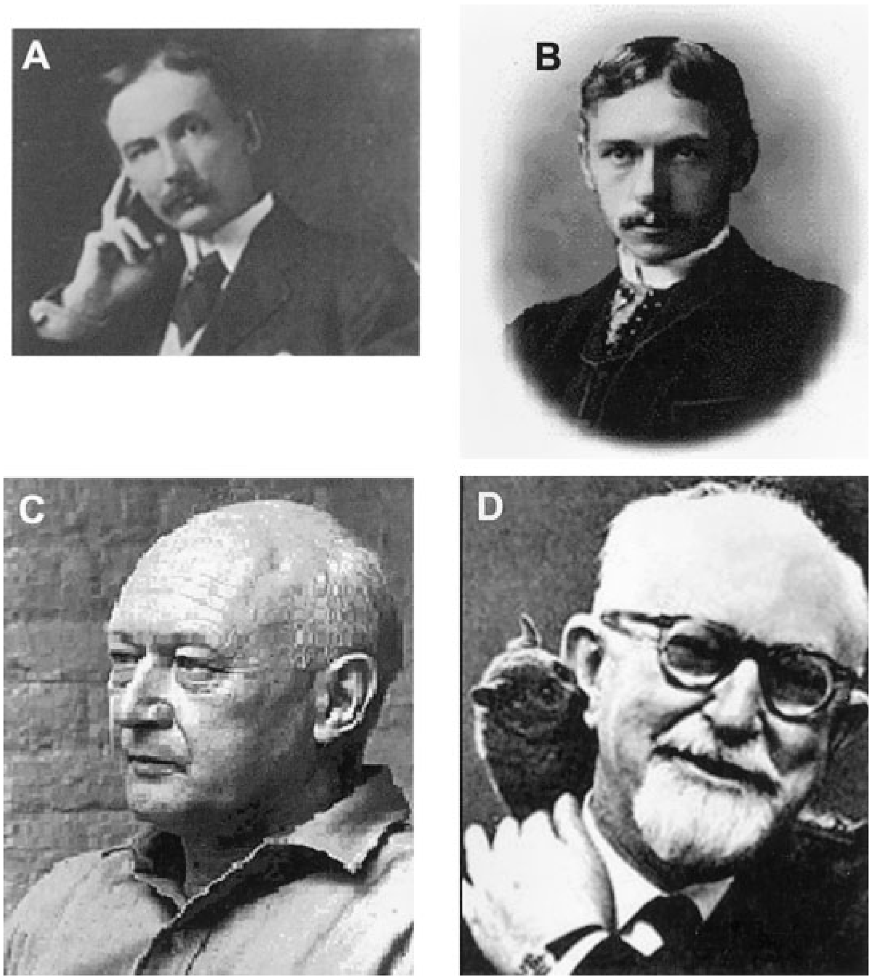

Figure 1. James Mark Baldwin, Henry Fairfield Osborne, C.H. Waddington, G.G. Simpson. Sources: reprinted with permission from (A) http://www.psych.utoronto.ca/museum/baldwin.htm, University of Toronto, (B) American Museum of Natural History, (C) http://www.cecs.ed.ac.uk/graphics/waddington.gif Centre for the Study of Environmental Change and Sustainability, University of Edinburgh. (D) from.[2]

tirely avoid, the contending Darwinian and Lamarckian processes.

Evolution may depend on genes, but selection works through phenotypes and not all phenotypes are direct translations of genotypes. Animals respond to experience in ways that may be enabled, but not directly specified, by their inherited genome. Genomes have plasticity, as homeostatic, dynamic, responsive entities. An organism responds to its environment by learning through natural biofeedback how to maneuver through life, adjusting to physical, as well as social conditions. Many developmentally acquired traits, including psychological traits and behavior, can be *socially* inherited, as part of the environment if not the genomes of the next generation. If developing such a trait confers survival advantage, it will persist and proliferate in the population.

That's Lamarckian but without his incorrect genetic mechanism. But then how can such traits acquire a genetic basis as many—especially hard-wired instincts—seem to do? Baldwin's notion was that "the adaptive [developmentally acquired] modification acts . . . as a screen to perpetuate and develop congenital [genetically specified] variations . . . "[3] That is, genetic variation that conferred a partial or precursor state might be maladaptive and unable to proliferate on its own. But that variation could be shielded from selection and proliferate when it arises by chance in individuals who have acquired a similar advantageous state behaviorally. Over time, what was originally *ontogenetic* can become *phylogenetic*. Neither Lamarckian nor Darwinian selection is involved.

As a Princeton student in the 1880s, Baldwin participated in seminar discussions about these topics with Osborn, who was then a professor there. By 1897 Osborne had moved to Columbia and Baldwin was back at Princeton as a faculty member, when a somewhat polite, subtly one-upping priority dispute between them[1] appeared in the pages of *Science* (n.s. vol. v: 634) and *Nature* (vol. 55: 558). Most likely this was one of those scientific coincidences, which different investigators reach notions that are "in the air" but each thinks he was first.

Coincidentally, in 1896 there was also a report that environmentally heat-stressed pupae emerged as butterflies with altered wing patterns that resembled invariant and presumably "congenital" (to use Baldwin's term) patterns found elsewhere in the species' range (Figure 2).[5] By a half-century later, the evolutionary transition from environmental to genetic determination had been demonstrated experimentally by C.H. Waddington, who called the process *genetic assimilation*. G.G. Simpson[6] showed how the Baldwin Effect could be compatible with the standard genetic theory of natural selection. He thought this was peripheral to evolution, but Waddington argued it was a ubiquitous factor "since the properties with which [selection] is concerned are always phenotypic . . . products of genotypes interacting with environments."[7] Genetic assimilation has since been observed empirically and treated theoretically by many others and has even attracted the interest of computer scientists exploring mechanisms for adaptive machine learning.

Organismal Selection: Choosing Rather Than Chosen

Behavior is usually viewed as an evolutionary way of getting ahead, but the primary object of a lot of behavior is simply getting, without worrying

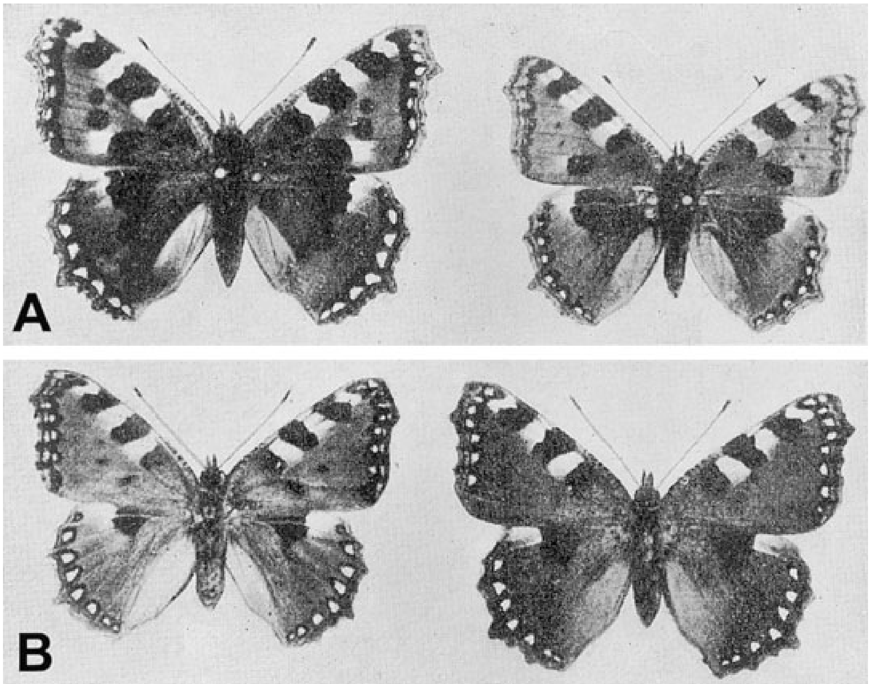

Figure 2. Application of heat shock to developing *Vanessa urticae* butterflies produces environmentally induced mimics (phenocopies) of "genetic" (normal) variants from other geographic areas. (A) Normal central European variant (B) heat-shock variant from central Europe resembling the normal Sardinian form. After;[4] for a good discussion see http://zygote.swarthmore.edu/env5.html.

about who's there first. Organisms looking for a good meal seek and occupy aspects of their environments for which they are individually suited. Behavioral self-sorting of individuals into subenvironments or lifeways they individually prefer could, but need not, involve Darwinian competition and differential fitness. In this sense animals can simply do what they do best, each group fertile and content. We can call this *organismal selection* to denote individuals aiming at targets rather than environments calling the shots.[1]

Complex life can be viewed as a continual, mutual seeking process to find a fit between varying environments and varying, mobile, sensing, purposive organisms. This is not a new idea. In Darwin's famous 1857 letter to Asa Grey (read the following year along with Wallace's Ternefine letter as the first public presentations of the idea of evolution) he said, "the varying offspring of each species will try . . . to seize on as many and as diverse places in the economy of nature as possible." In the *Origin* he said that "it is difficult to tell . . . whether habits generally change first and structure afterwards; or whether slight modifications of structure lead to changed habits; both probably often change almost simultaneously." If organismal selection leads similar organisms to find themselves in similar areas, mate there, and their offspring stay around, the result can be what Darwin or Wallace might have called a local persistence of "type."

SYMPATRIC SPECIATION

Behavioral sorting of this kind can contribute to *sympatric* speciation, that does not require a physical mating barrier. Sympatric speciation might account for the multiple closely related species living in essentially the same place, so commonly observed, especially in the tropics. But sympatric speciation has been considered heretical for at least three reasons. Sewall Wright in the 1930s showed that under simplifying equilibrium assumptions even a trickle of gene flow limited the degree of genetic divergence that would accumulate between populations. At about the same time, Ernst Mayr declared that geographic isolation was necessary for speciation. And there has been an almost automatic Darwinian assumption that speciation is due to natural selection.[9] Nonetheless, the sympatric speciation may not be too far off-target.

A classic test case for behaviorally induced diversification is the apple maggot (actually, a fly), *Rhagoletis pomonella,* and this ties us into another Wild West story, that of John Chapman—Johnny Appleseed—who traveled west across the country in the early 1800s spreading apple trees. By 1867, B.D. Walsh[10] noticed that some *Rhagoletis* flies had expanded from their native host plant, the hawthorn, to the domestic apple as a new host. *Rhagoletis* flies lay their eggs on their preferred host, and the hatchlings tend to spend their lives there, learning olfactory cues that reinforce their preference. Flies on either host are morphologically similar and competent to occupy the other host, though they typically don't. However, apples and hawthorns have slightly asynchronous fruiting stages, and a correlation has developed between that and the eclosion (adult emergence from pupa) times of the respective *Rhagoletis* subpopulations. Recent studies have identified genetic variation that is associated with developmental timing. This may presage a future genetic isolating mechanism, but flies have al-

Figure 3. *Rhagoletis pomonella.* Photo courtesy Jeffrey Feder. (http://www.science.nd.edu/biology/faculty/feder.html)

[1] I've used this term elsewhere, but only in writing this column did I discover that the idea was articulated by Lutz in 1948.[8] Baldwin used the term "organic selection," but that referred to adaptive response to, rather than choosing among, environmental conditions. A related ecological concept is known as "niche construction."

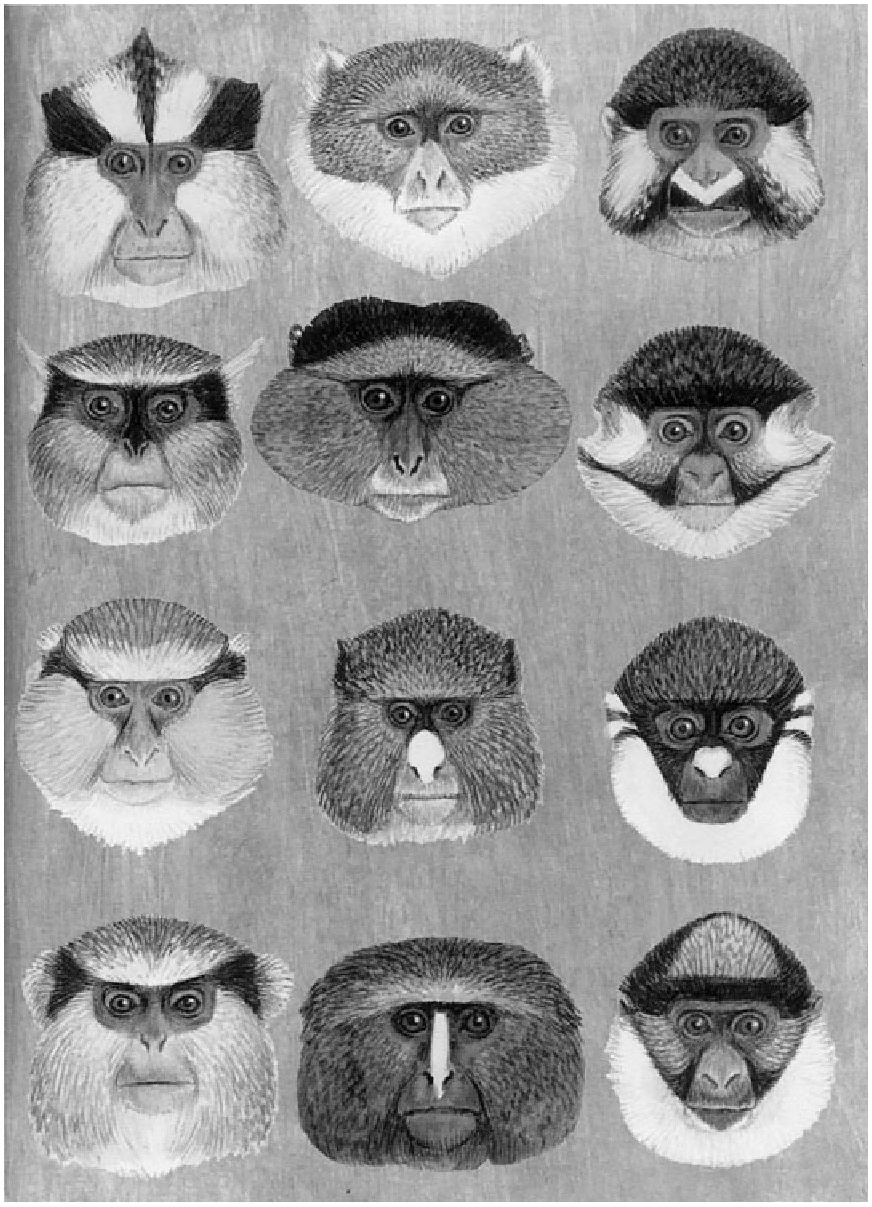

Figure 4. African monkeys. Guenon faces. Reprinted with permission from.[12]

ready specialized while both populations are polymorphic for this variation, so selection is clearly not necessary. Since the populations have never been geographically isolated, they seem to represent sympatric divergence caught in the act.

Sympatric speciation also seems to have been occurring among cichlid fish in Lake Victoria and other lakes in Africa and the Americas. Local cichlid variation includes color differences associated with assortative mating and feeding-related morphology. Genetic data suggest that the incipient speciation has been recent and rapid. What combination of dietary, mate preference, or other factors is responsible is unclear, but organismal selection seems to be one of them. Overall, sympatric speciation now seems to be supported by both theoretical and empirical evidence.[11]

Primate and Human Evolution

These ideas are highly relevant to primate and human evolution. Organismal selection may be important to what primates, with their highly capable brains and discrimination powers, have been doing to get where they are today. Multiple species of similar primates often occupy roughly the same area, largely varying in ways related to behavior, like diet or preferred parts of the forest canopy. For example, variation in color vision may be partly responsible for leading animals towards areas rich in what they can see. The exotic variation in coloration pattern, shown for African guenons in Figure 4, may be used by the animals to aggregate with others whose similar patterns or related signaling behavior are familiar to them since birth.[12]

When it comes to behavior, humans are of course the most interesting of all. Loring Brace used to characterize *culture* as the hominid ecological niche. In the face of claims of multiple contemporary hominid fossil species—perhaps like African monkeys and apes today—he invoked the competitive exclusion principle of ecology to argue that there could only be one culture-bearing hominid at a time. This notion supported the single-species hypothesis for which the Michigan school, in which I was trained, was long noted (and/or notorious). The competitive exclusion principle is not so widely applied as it once was, but one can turn the argument somewhat on its head to suggest that the flexible nature of culture could serve as a vehicle for organismal selection to *enable* hominids to find, or make, local isolating mechanisms leading to multiple sympatric subspecies or even species. Ritual display and language are obvious potential examples.

The genetic processes responsible for human evolution will be interesting to discover, and many investigators are looking for them. Recent candidates have included a gene called *Foxp2* that may be related to language, and/or a general increase in gene expression levels in the human brain. A focus on intelligence is perhaps rather arrogant, when we know that thumbs, and pelvic and limb structure, hairlessness, pubic patches, protuberant breasts, altricial fetuses, dull teeth, olfactory and vision changes, also differentiate us from our nearest relatives. But all these changes involve behavior or are its consequences.

Genetic Sources of New Traits

Several recent genetic studies may contribute to a new understanding of how, despite previous theoretical assumptions, speciation might be possible without geographic isolation. Chromosomal rearrangements that occur in local groups previously sorted by organismal selection or other means can facilitate subsequent speciation even in the presence of gene flow.[13] In hybrid individuals produced by mating between individuals from two subpopulations, recombination is inhibited in the rearranged chromosomal regions but not in non-rearranged regions. Gene flow can continue in the latter, but not the former regions, whose genes can constitute a sequestered reservoir for the accumulation by chance, organismal or natural selection of locally-specific variation. Eventually, enough genetic variation can build up to provide a standard mating barrier. There is suggestive evidence for this phenomenon in the evolutionary divergence of humans and chimpanzees.[13,14]

Rearranged chromosomal regions in *Rhagoletis* contain genes whose variation is related to developmental timing and hence correlated with their plant preferences.[15] Johnny Appleseed planted apples as cider kits for thirsty colonists moving to the Wild West, but the variation that enabled some *Rhagoletis* to bob for apples may have arrived by gene flow moving to the Wild North from Mexico, where the variation becomes available as a means of behavioral sorting.[16]

Primates can form hybrids where two species' ranges overlap. The classic example is the anubis-hamadryas baboon hybrid zone in the Awash region of eastern Africa studied for many years by Cliff Jolly and Jane Phillips-Conroy (Figure 5). One might expect hybridization to facilitate gene flow and homogenize the species. But the narrow hybrid zone has not expanded, and thus maintains a partial isolating barrier despite continued interbreeding. It appears that outside the hybrid zone itself, familiarity breeds content, and the new-looking hybrid animals have little sex appeal (C. Jolly, personal comm.). Thus, genetic variation that affects mate-choice behavior or appearance does not diffuse from the hybrid zone to unify the species. However, after a generation of segregation and recombination, *other* genetic variation can end up in normal-looking individuals and slip undetected into the hinterlands. Here organismal selection fills the role served by chromosomal inversions in the human-chimp example.

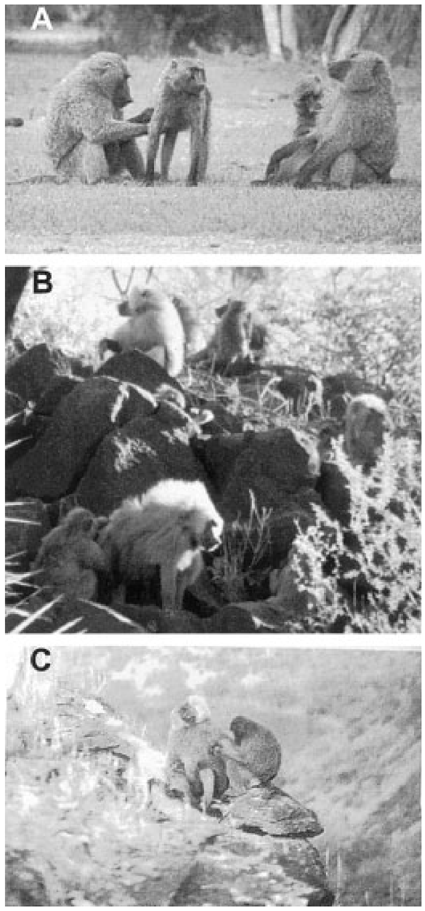

Figure 5. Hybrid baboons. A. Anubis; B. Hamadryas; C. An anubis-like female grooming a hybrid male. Courtesy J. Phillips-Conroy.

In these various instances the isolating barrier is not the result of natural selection (e.g., for big brains, big manes, or apple-fancy). It is in this sense that Baldwin and others claimed evolution could occur without selection.

DEVELOPMENTAL SYSTEMS THEORY

Baldwin's notions have persisted as a kind of biological backwater with essentially unchanging underlying logic for a century, perhaps reinforced at a low level by an equally persistent failure to reduce ontogenetic behavioral phenomena and developmental psychology to genetic terms. But the Baldwin Effect is having something of a revival. One current incarnation is called *developmental systems theory* (DST).[17,18] Reminiscent of some of the early work on assimilation, proponents point to traits that are universally observed in natural populations of a species that thus seem to be instinctive and phylogenetically programmed—like response of bird hatchlings to species-specific vocalizations—but that can be shown experimentally to be learned rather than specified by genes.

To say that genes are ultimately responsible for such traits because plasticity is built into genome is an evolutionary truism but not very helpful in explaining the phenomena. There is an undeniable tension between the DST view and the drive in sociobiology to find genetically prescriptive behavior resulting from selection. Many DST proponents are unhappy with endless nature-nurture dichotomy and seek a unifying view. Organismal selection and genetic assimilation could provide it, one reason DST people are interested in apple maggots. But the conflict between nature and nurture involves broader, long-standing worldview differences that are unlikely to be resolved any time soon.

SHOOTING STRAIGHT, BUT KEEPING ON TARGET

Baldwin and others were groping to reconcile competing ideas about evolution. Darwin himself held some Lamarckian notions, but natural selection won, and a consequence was that phenomena like the Baldwin Effect never enjoyed mainline attention. Its ideas persist because behavior is not simply a contest between organisms and a distinct, separate environment that screens them. In many ways facultative behavior—making judgments and choices—is the *essence* of animal life, and makes, as well as responds to, its circumstances. I won't shock any anthropologists by saying that human behavior and culture not only are traits that resulted *from* evolutionary forces, but traits *par excellence* that in turn *shape* those forces directly. Much of our biological nature is the result of a million or more years of life in a culture-bearing environment.

Genetic evidence suggests that evolution is not just about natural selection, but is generally a dynamic interplay of weak forces, consistent with the stepwise models for the incremental evolution of complex traits. Natural and organismal selection along with drift—screening, sorting, and luck—are all commonly present. Depending on the circumstances, they may have effects of comparable relative strengths, which may be everchanging. If we were to look as earnestly for evidence of organismal selection as we do for natural selection, we might actually find it, and it might be enlightening.

There is an interplay between simply doin' what comes natur'lly and being punished by oblivion for not doing what nature wants. Both involve sorting of genotypes and local changes in the relative frequencies of genetic variation. Both can contribute to speciation. If we are Man the Hunter, then Annie Oakley was not "adapted" for hunting. That was how Frank Butler felt when reluctantly forced into a shooting contest with her. Annie's mom may have been adapted to baking biscuits and tending the chickens and kids, but Annie adapted to what *she* could do. Apparently, although "you can't git a man with a gun," her behavior did enhance her Darwinian fitness—she found an adaptable man:

> You don't have to know how to read or write,
> When you're out with a feller in the pale moonlight.
> . . . .
> Still they raised a family, doin' what comes natur'lly.

However, I've been writing about the evolutionary effect of purposive behavior, and it can be subtle: in the end, Annie had to miss a few shots intentionally to get what she was aiming for.

NOTES

I welcome comments on this column: kenweiss@psu.edu. I have a feedback page at http://www.anthro.psu.edu/weiss lab/index.html, where a more complete set of specific references can be found. I thank Anne Buchanan, Sam Sholtis, and John Fleagle for critically reading this manuscript, and Alan Walker, Cliff Jolly, and Jeffrey Feder for helpful interaction.

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