Nabokov's Evolution

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Nabokov: The highest enjoyment is when I stand among rare butterflies and their food plants. This is ecstasy, a sense of oneness with sun and stone.

. . .

Interviewer: Is there any connection [of lepidoptery] with your writing?
Nabokov: There is in a general way because I think that in a work of art there is a kind of merging between the two things, between the precision of poetry and the excitement of pure science.

—Emma Boswell, *How Do You Solve a Problem Like Lolita?*

Much has been written on Nabokov's views on evolution, the origin of species, and, especially, mimicry in nature. Nabokov scholars hold a diversity of opinions, veering from defending Nabokov's heterodox beliefs about evolution to criticizing him for not fully accepting the modern evolutionary synthesis developed in the 1930s and 1940s in Europe and North America.

Nabokov the scientist was maybe a little old-fashioned in his methodology, even for his time, concerned mainly with morphological systematics. He evinced a profound dislike for applying statistics to his science. Nabokov furiously rejected a statistical criticism by F. Martin Brown of his work on "scale rows," a method he invented for the study of plebejine butterflies.[1] His lack of appreciation of applied mathematical theories of evolution probably ensured that he could not form a strong opinion about the works of Ronald Fisher, J. B. S. Haldane, and Sewall Wright, the founders of the modern synthesis of Mendelian genetics and Darwinian natural selection. However, Nabokov would certainly not have been alone among biologists of his time in his contempt for the modernization of biological science and, in particular, of mathematical or genetic approaches to systematics.[2]

Nabokov certainly understood much better the later part of the modern synthesis on species concepts and speciation, beginning in 1937 and continuing in the early 1940s largely by another triumvirate. Their leader was a fellow Russian, the geneticist and former beetle systematist Theodosius Dobzhansky. Julian Huxley from England—the grandson of "Darwin's Bulldog," Thomas Henry Huxley—and Ernst Mayr, Nabokov's own scientific colleague at the Museum of Comparative Zoology from 1953, completed the trio. Nabokov would certainly have perused the systematics-oriented book by Mayr.[3] This second wave of the modern synthesis was important in connecting systematics and natural history with the new mainstream of genetics and evolutionary thought. Nabokov criticized these ideas, mainly in unpublished documents.

Instead of attacking or defending Nabokov's views on mimicry and species concepts, I merely comment here on his views from a scientist's viewpoint. The modern synthesis was a broad church, and different players in the formation of the synthesis had varying opinions; my perception is that his views were not particularly extreme at the time. Others have al-

ready excellently described Nabokov's observations on these matters.[4] I hope to contribute a clearer understanding of Nabokov against the scenery of scientific thought in his day. Ideas not dissimilar from Nabokov's apparently heretical stances were already present in the 1940s and, indeed, have led to the progression toward today's understanding of biology.

ALTHOUGH A POTENTIALLY GREAT SCIENTIST—he might well have developed into a major systematist of butterflies had he not proved a highly successful novelist —Nabokov did not fully put his science together with his art. To many Nabokov scholars, this may seem a hard argument to swallow. Nabokov expended many words in telling his public how he embodied a fusion of art and science (see the epigraphs to this essay). And late in life he snobbishly argued that C. P. Snow's *Two Cultures* represented only a slight divide between lowbrow literary culture (presumably, he disapproved of Snow's novels) and trivial utilitarian science. Nabokov certainly was a good systematist, and yet he somehow believed that mere mechanical understanding is less sublime than the appreciation of the "non-utilitarian delights" of nature. To a scientist as well as to Nabokov, the beauty and intricacy of the underlying structure hold the greatest wonders in life.[5] To explain these mysteries is the goal of science, but this is most convincingly achieved in the mathematical language of mechanics and dynamics, and data are best analyzed by means of reference to some statistical model, rather than solely through verbal discussion.

Many biological mysteries remain, of course. Only by rational and theoretical exploration of these mysteries, rather than by rejection of the possibility of rational explanation, does science progress. Nevertheless, in science as in art, imagination and chance are keys to exploring mysteries. Without imagination, advances in scientific understanding outside the prevailing paradigm would be impossible, and science would grind to a halt.

As Karl Popper argued, the source of a scientific hypothesis is often completely nonscientific and may even stem from religious conviction. Johannes Kepler's discovery of approximately elliptical planetary motions was motivated initially by a Neoplatonic, almost religious notion: The Copernican idea that the Sun in the universe plays the same role as the Good plays in the realm of ideas. The Sun could not be expected to revolve around the Earth under this system. Orbits of mere planets like Earth (and its inhabitants) should instead move at constant angular velocity in obedient and perfect circles around the Sun. Tycho Brahe's detailed observations of the orbit of Mars, elliptical and showing variations in speed, ruled this model out, to Kepler's evident astonishment. Clearly, the initial hypothesis that led finally to Kepler's ellipses was imaginative rather than scientific or empirically based.[6] Imagination and aesthetics can thus be enormously helpful in science. But they can also hold science back. Galileo himself never accepted Kepler's eccentric planetary orbits because of the loss of perfection, just as Einstein was to reject the notion of God throwing dice with respect to quantum mechanics four centuries later. It would be unsurprising for Nabokov to have a similar weakness.

Before discussing the topics of mimicry and speciation in detail, I should like to propose that, in his dissatisfaction with the modern synthesis, Nabokov displays a blend of imagination and critical thinking likely to have been useful in making great scientific discoveries. He became a great novelist, but there is no reason, had he not given up active science and had *Lolita* not sparked a huge new readership, why he might not have become much

more revered as a butterfly taxonomist instead. Among his abandoned projects were field guides. He certainly was capable of writing definitive field guides, such as to the butterflies of North America before Alexander B. Klots and the butterflies of Britain and Europe before L. G. Higgins and N. D. Riley. As it turned out, Nabokov was reduced to writing well-informed reviews of both books.[7]

IN MY VIEW, NABOKOV DID GET MIMICRY WRONG, but he certainly did not deny the importance of natural selection in general, and most of his attacks on mimicry were in any case literary flourishes not to be taken too seriously. For example, some of the literary examples of mimicry stories that seem too good to be true for the narrator in "Father's Butterflies" are simply that—Nabokov invented them for this purpose, as Dieter Zimmer has shown. In one case, a fictitious moth, complete with Latin binomen, is invented. In another, the extraordinary caterpillar of a real species, the Lobster Moth (*Stauropus fagi*) actually does go through an antlike as well as a lobsterlike stage, but Nabokov has added an extra stage that mimics bird lime, which other caterpillars (particularly of *Papilio* butterflies) do have.[8]

What formed Nabokov's views on mimicry? Like Nabokov, I became fascinated at an early age by mimicry, triggered especially by butterfly and moth adaptations. My first encounter was through books: Walter Linsenmaier's panoramic illustrations in a child's *Time-Life* book about evolution. As well as camouflage, Linsenmaier's images depicted mimetic *Heliconius* and ithomiine butterflies flying in the *Araucaria* forests of coastal Brazil. When, at boarding school, I started rearing caterpillars of moths and butterflies, camouflage became obvious. The "twig" caterpillars of the Peppered Moth (*Biston betularia*) and other geometrids were extraordinarily convincing to this young vertebrate. Even the most mundane and tiresome environmental features are copied: an astonishing array of creatures mimic bird shit. For example, moths like the Chinese Character (*Cilix glaucata*) or the Lime-Speck Pug (named after "bird-lime," of course; *Eupithecia centaureata*), or caterpillars, such as a number of young *Papilio* caterpillars. I yearned for the diverse rainforests of South America, where mimicry and camouflage seem most highly developed. It's probably no accident that I now study *Heliconius* and ithomiines in my professional career. To those of us with a similar background, it's easy to understand how Nabokov became fixated on a phenomenon first encountered in the crystalline clarity of childhood memories. He had seen the same caterpillars and imagos closely resembling leaves, bird droppings, and twigs that I had, and more.

Nabokov knew that explanations of mimicry were to be found in natural selection. As a child needing to identify his catches, he read natural history books that would have invoked natural selection to explain camouflage and mimicry. He certainly read Darwin (see *The Gift*), and he seems to have accepted Batesian and Müllerian mimicry of unpalatable species as having some utility and involving natural selection.

Nabokov's real complaint about "utilitarian explanations," as he liked to label natural selection, was with camouflage, rather than true mimicry. How could a blind mechanical process lead to such minutely detailed resemblances to such piffling features of the environment? Camouflage, sometimes dubbed "masquerade," is regarded by biologists to be distinct from actual mimicry—the copying of simple but garish warning patterns by mimic species that predators actively avoid. Detailed camouflage is instead the copying of things

in the environment that predators normally ignore or overlook. The difference is that a mimic copies a signal, whereas in masquerade, the copied item (for example, a twig) is normally not in itself designed by natural selection as a visual signal.

Camouflage, the mimicry of features of the environment, such as the transparent spots in a butterfly wing imitating fungus-eaten holes in dead leaves (see Color Plate E5), to Nabokov seemed too perfect and too complex to have been effected by predators discriminating against deviants over long stretches of geological time. In his opinion, this cried out for something less chancy than a mere mechanical process of natural selection based on initially random mutations, for which "a trillion light years would hardly be sufficient."[9] Nabokov was here (at least in "Father's Butterflies") using something like the classic "argument by design" adopted by William Paley and the natural theology movement of the early nineteenth century. If you find something like a watch in a field, you know it was designed because of its function. Unfortunately for us, who would like to access Nabokov's actual beliefs, he explores the theme in much greater detail in his preserved imaginative rather than in factual writing.

Nabokov was no creationist. He was an iconoclast—not unheard of among evolutionary biologists, let alone novelists. Many other mainstream biologists have argued and still do argue against strictly selective explanations of mimicry.[10] Some scientists still doubt the camouflage explanation for the evolution of the black, or melanic, form of the Peppered Moth during the Industrial Revolution.[11]

I speculate that Nabokov was a victim of literary enthusiasm rather than a real disbeliever in the power of natural selection to effect the many minute changes that result in extraordinarily accurate mimicry. Nabokov's opinions are often strongly expressed. Perhaps Nabokov just didn't like to prevaricate or hedge enough for the scientists. In his literary treatment of mimicry, we should be aware that he was perhaps enunciating controversial views that might have been true in an alternative world, rather than always stating what he actually believed about nature.

IN 1944, NABOKOV PILLORIED THE MODERN synthesis species concept in unpublished notes by arguing that morphology should trump mere mating preference: "This is the kind of nonsense that you finally get with these subtle experiments with geneticists."[12] Here is a clear reference to Dobzhansky's view of species, the "biological species concept." Dobzhansky's concept, based on "reproductive isolating mechanisms," was triggered by his discovery of "race A" and "race B" of *Drosophila pseudoobscura*.[13] Apparently identical in appearance, they differed in chromosomal arrangements, as well as in strong mating preferences and partial hybrid sterility. To Dobzhansky, they were real species, not mere races, and race B was later named *Drosophila persimilis*.[14]

That the two are real, separate species is now widely accepted. However, the Dobzhansky-Mayr view was controversial in 1944. Even Alfred Sturtevant, who had been a senior colleague of Dobzhansky's in Thomas Hunt Morgan's laboratory, disagreed with the need to consider the two as separate species. He argued that the "race A" and "race B" designations were sufficient "in identifying wild specimens without breeding from them or examining their chromosomes."[15] Sturtevant was not a lonely Luddite; he was one of the world's best-

known geneticists at the time. As an undergraduate in Morgan's lab, he had developed the key method, still used today, for mapping genes along chromosomes.

In his critique, Nabokov seizes on logical weaknesses in the biological species concept of the modern synthesis. I do not agree wholly with his attack on geneticists and their species concept, but he was not alone. In his practical application of ranks to butterflies, Nabokov's species concept seems to me close to the mainstream of the other modern systematists of his time. Today, the Mayr-Dobzhansky view of species is under more critical attack than ever. In terms of basic, practical taxonomy, many of us today hold views similar to those of Nabokov sixty years earlier.

An important way genetics impinged on Nabokov's butterfly systematics was via chromosome counts. Nabokov was always against succumbing "to the blandishments of the chromosome count" in butterfly systematics, on the grounds that their use would make species identification prohibitively difficult.[16] This is not dissimilar to Sturtevant. On the other hand, Nabokov's genitalic dissections require microscopes, albeit of lower power than those used in chromosomal studies. Both suffer from the same invisibility problem for the fieldworker. And surely it is more important to know what a taxon itself really is rather than to constrain one's viewpoint to a single mode of human perception?

Taxa with different chromosome numbers or genetic traits which appear to be reproductively isolated tend also to have subtle differences in morphology. Nabokov excelled at the study of color pattern and genitalic morphology and knew a great deal about butterflies, particularly the Polyommatini. In my somewhat inexpert opinion, the Polyommatini Blues, including *Plebejus, Aricia, Lysandra,* and *Agrodiaetus,* among others, are a mess of closely related small butterflies. Many species hybridize with one or more other species or even across genera, and they are all similar in overall morphology, though they can differ in color pattern. Nabokov did a great deal to sort this group out, especially in the Americas.

So how did he classify species in practice? Many philosophical papers have been written about species concepts, especially since the modern synthesis. Dobzhansky and Mayr in their work felt that they had rescued the pre-Darwinian idea that species were real, by which they meant objectively definable. Darwin and the early Darwinists had instead argued that although species can emerge and become more distinct over evolutionary time, there is no objective reality: we humans must decide where to cut the continuum, and what groups to demarcate as species. Mayr and Dobzhansky did not believe that species were defined by a Creator; their new objective reality was instead reproductive isolation. Both were able to maintain that species were discretely different from varieties (or races) within species, even though both agreed that species almost certainly evolve apart somewhat gradually. Mayr in particular reviewed the extensive evidence for hybridization between "good" species, and of subspecific or ecological races, incipient almost-species within these real species.[17] However, lacking molecular genetic markers (invented in the late 1960s), Mayr was able to brush difficult intermediates under the carpet. Hybridization was interpreted to be largely a pathological by-product of human-altered environments. In contrast, most or all subspecific ecological races that co-occurred in geographic overlap (or "sympatry," to use Mayr's term) were seen as plastic rather than genetic variants, or sometimes as by-products of hybridization after secondary contact between formerly geographically isolated (or "allopatric," in Mayr's terminology) good species. Mayr was adept at obfuscating the logical difficulties of his views. Although he cited reproductive isolation as the definition and con-

cept, his species taxa were inferred largely from natural populations based on morphology. Species were deemed separate if there were few or no morphological intermediates (that is, putative hybrids) between them in areas of sympatry. If there were plenty of intermediates in areas of overlap, then the different-looking taxa were deemed to be varieties or geographic races within a single species.

One of the features of Mayr's definition that Nabokov seized on for criticism was a statement about geographically separated populations. Here the test of morphological intermediates was not possible, and so Mayr fell back on an inference of "potential interbreeding." As Nabokov realized, this meant in practice that morphological studies alone were the actual systematic tools. As for the occasional cases of hybrids in nature among good species, Mayr was somehow able to argue the "reproductive isolation" definition always held, even in taxa that didn't show it very well; to Mayr, these troublesome cases were mere exceptions that proved the rule.

The Mayr-Dobzhansky view of species became greatly celebrated, almost revered—and it still is—because it seemed to provide new and solid meaning in an area, the understanding of species, that had supposedly been laid waste by the Darwinian revolution. Nonetheless, systematists actually working at the coalface of taxonomy, like Nabokov, were not helped by these theoretical and genetic arguments for species reality. They still had to parse the actual morphological continuum into species, especially in difficult groups. Practically, the only important question about someone's systematics is not about beliefs but about what is done with those beliefs. All that really matters about Nabokov's productive work on butterflies is the question: Was he a lumper or a splitter? The American lepidopterist W. J. Holland characterized the differences between splitters and lumpers in a book that Nabokov almost certainly read:

> A "splitter" magnifies the importance of trivial details; he regards minute differences with interest; he searches with more than microscopic zeal after the little things and leaves out of sight the lines of general resemblance. . . . The labors of such naturalists may be highly entertaining to themselves, but they are, to say the least, provocative of unpleasant feelings in the minds of others who come after them and are compelled to deal with and review their labors.
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> The "lumper," on the other hand, is a man who detects no differences. . . . Any two moths which are of approximately the same size and the same color, are, by him, declared to belong to the same species. . . . His genera are "magazines," into which he stuffs species promiscuously. The "lumper" is the horror of the "splitter," the "splitter" is anathema to the "lumper"; both are the source of genuine grief and much hardship to conscientious men, who are the possessors of normally constituted minds and truly scientific habits.[18]

In his published work, Nabokov expounds on his species concept and politely argues that it must differ from Mayr's and Dobzhansky's focus on biology:

> The strictly biological meaning forcibly attached by some modern zoologists to the specific concept has crippled the latter by removing the morphological moment to a secondary or still more negligible position, while employing terms, *e.g.*, "potentially interbreeding" that might make sense only if an initial morphological approach were presupposed. What I term species, in my department,

> can be defined as a phase of evolutional structure, male and female, traversed more or less simultaneously by a number of, consequently, more or less similar organisms morphologically shading into one another in various individual and racial ways, interbreeding in a given area and separated there from sympatric representatives by any other such phase by a structural hiatus with absence of interbreeding between the two sets. . . . It may happen that two structurally distinguishable local forms belong to one species allopatrically because they racially intergrade, but at the same time belong to different species sympatrically because in some other region their structural counterparts occur side by side without interbreeding (this incidentally is the position in *Lycaeides*). In such cases one should give precedence to the all important sympatric moment and find somewhere in the spirals of racial intergradation a point at which the whole system can be elegantly . . . divided into two parts, *i.e.*, two species, using some combination of trinomials.[19]

In this, Nabokov displays a useful and informed systematic approach. He clearly recognizes logical flaws in Mayr's writings, but an underlying morphologically based practical approach is accepted (Mayr himself inherited his similar methods from David Starr Jordan, Walter Rothschild, and Rothschild's curators of birds and butterflies—Ernst Hartert and Karl Jordan, respectively—who instituted in systematics a practical version of the biological species concept in the years 1890–1915). By the time Nabokov was actively classifying butterflies, the accepted Linnaean binomial nomenclature (genus, species) had become trinomial (genus, species, subspecies). This practical revolution allowed the inclusion of geographic races or subspecies within a broader species and aided the understanding of relationships and classification. It was the nomenclatural revolution, rather than the purely theoretical reproductive isolation definition, that was the real advance of the twentieth-century species concept. Nabokov embraced this practical advance along with Mayr while maintaining his opposition to the logic used in its defense.

In summary, Nabokov, judged by his practical systematics, would have been deemed by Holland a possessor of a "normally constituted" mind and "truly scientific" habit.[20] He was a product of his times, and he was neither a lumper nor a splitter. His disagreement with genetics and chromosomal information might be criticized (although this was, in his defense, before reliable genetic markers became available), but his disagreements over species with Mayr have, in my view, considerable relevance today. Overall, he resolved his views in a way that made his revisions extremely useful, even for much later generations of butterfly researchers.

Notes

1. Nabokov, "Remarks."
2. Huxley, *Evolution: The Modern Synthesis.*
3. Mayr, *Systematics and the Origin of Species.*
4. *NB; NBl;* Zimmer, *Guide.*
5. *NB,* 399.
6. Popper, *Conjectures and Refutations.*
7. Nabokov, "World of Butterflies," and "Rebel's Blue."
8. See http://www.d-e-zimmer.de/.
9. *NB,* 223.
10. Goldschmidt, "Mimetic Polymorphism," and "Mimetic Polymorphism (Concluded)."

11. For recent discussions of this long-standing controversy, see reviews by Cook et al., "Selective Bird Predation," and Grant, "Industrial Melanism."

12. *NB*, 308.

13. Dobzhansky, *Genetics and the Origin of Species*.

14. Dobzhansky and Epling, *Contributions*.

15. Sturtevant, "*Drosophila pseudoobscura*."

16. Nabokov, "Rebel's Blue."

17. Mayr, *Systematics*.

18. Holland, *Moth Book*, 112–13.

19. *NB*, 353–54.

20. Holland, *Moth Book*, 112–13.

The Leafwing butterfly, *Zaretis isidora*, photographed in Corcovado National Park, Costa Rica, 1981, reared from caterpillar by J. Mallet