

GETTING RIGOROUS ABOUT DEVELOPMENTAL INSTABILITY

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The Mysterious Mr. Smithson

The Stranger and the Statesman: James Smithson, John Quincy Adams, and the Making of America's Greatest Museum: The Smithsonian. Nina Burleigh. William Morrow, New York, 2003. 320 pp., illus., \$24.95 (ISBN 0060002417).

In late August 1838, after an arduous six-week voyage, the American lawyer and diplomat Richard Rush finally stepped off the packet ship *Mediator* and onto terra firma in New York. He did so with a sense of immense relief, for he was finally leaving behind not only the seasickness that had plagued him since the ship left London but also the long ordeal preceding his grueling transatlantic passage. For the previous two years Rush had patiently, methodically, and (in the end) successfully struggled to gain control of a bequest that the British scientist James Smithson had granted to the US government. Among the items in Rush's possession on his triumphant return home were Smithson's extensive mineral collection, a modest library, scientific notes, various personal effects, and the most compelling reason for his lengthy stay in England: 105 sacks of gold sovereigns valued at more than \$500,000, the proceeds from the liquidation of Smithson's extensive property holdings. Within a decade after Rush's return, Smithson's bequest led to the founding of the Smithsonian Institution. Today that organization boasts an annual budget more than a thousand times greater than Smithson's initial gift, a visitation rate that is approaching 30 million people each year, and a reputation as one of the premier museum complexes in the world.

Written in vibrant, accessible prose, *The Stranger and the Statesman* presents the story of James Smithson, his unusual bequest, and the controversy it engendered. Smithson, born in Paris, France, in 1765, was named James Lewis Macie by his mother, Elizabeth Keate Hungerford Macie, a widow with aristocratic blood. He was the illegitimate offspring of

Hugh Smithson, later known as Sir Hugh Percy, who rose from a merchant-class background to become the Duke of Northumberland after marrying advantageously. His father, who never publicly acknowledged his paternity, was renowned for his excesses, including ostentatious displays of wealth and many illegitimate progeny. His mother, who was quite adept at using the courts to protect her financial interests, was apparently the source of young Macie's fortune. She was also the one who urged him to adopt the name of Smithson, which he did after her death in 1800.

When he was 17 years old, James Lewis Macie matriculated at Pembroke College, Oxford, where he not only showed an aptitude for chemistry and mineralogy but also engaged in his first serious fieldwork. The brilliant physicist Henry Cavendish, for whom Macie briefly worked as a laboratory assistant, served as one of his scientific mentors. Macie soon positioned himself as "a serious scientist" with a reputation for "scrupulous laboratory methods" (p. 105). Within a year after his graduation from Oxford in 1786, he gained election as a fellow of the Royal Society of London. By the time he died in 1829, he had published 29 scientific papers, most of which detailed the chemical composition of minerals and various other substances (including a human tear). In 1832 a form of calamine was renamed "smithsonite" in his honor.

Smithson, who had "always straddled the divide between curious gentleman and scientific professional" (p. 161), would probably rate little more than a footnote in the history of science were it not for the will he drew up when he was 61 years old. In it he left his entire estate to his nephew, the illegitimate son of his brother. If this young man were to die without a proper will, however, Smithson wanted his property to pass on to the "United States of America, to found at Washington, under the name of the Smithsonian Institution, an Establishment for the increase & diffusion of

knowledge" (quoted on p. 168). When his nephew died unexpectedly in 1835, this clause in Smithson's will came into effect.

Many mysteries surrounding Smithson's life remain, but perhaps the greatest is why he left his vast fortune to a nation he had never even visited. Also puzzling is exactly what kind of institution he hoped to see established under his name. Nina Burleigh, author of *The Stranger and the Statesman*, suggests that a clue to his intentions may be found in Smithson's role as a charter member of the Royal Institution, a scientific organization designed to bring scientific knowledge to the masses, with the hope of making them more efficient workers. Burleigh speculates that Smithson may have been motivated also by a desire to render his adopted name more famous than the Percy surname his absent, unsupportive father had eventually taken.

Whatever his intention, news of his will provoked intense controversy in the United States. Former president and later congressional representative John Quincy Adams had long hoped to see the federal government actively promote the pursuit of science in America. Consistent with that aim, he led a group of Northerners and Westerners who welcomed Smithson's bequest with open arms. However, they offered a bewildering variety of proposals for spending the money, ranging from an astronomical observatory to an agricultural college and from a national library to a national university. Most Southerners, on the other hand, strongly opposed accepting the money. They couched their opposition in terms of fears that the gift represented an affront to American honor, but the real source of their resistance was grounded in their staunchly pro-slavery, anti-federal views.

Ironically, the money that Rush brought over from England was lost when the federal government invested in a series of Arkansas state bonds that slid into default. An infuriated Adams then led a successful campaign to force the federal government to restore the Smith-

son fund to its original level, plus interest. Not until 1846, however, following long and sometimes acrimonious debate, did Congress finally agree to the terms establishing the Smithsonian Institution.

Journalist Nina Burleigh, who has written many popular articles and another book, *A Very Private Woman: The Life and Unsolved Murder of Mary Meyer*, has done a wonderful job of mining fresh archival sources to illuminate Smithsonian's life. Even so, her protagonist will probably always remain an enigmatic character, for the bulk of his personal papers were destroyed in a fire that engulfed "the Castle," the Smithsonian Institution's first building, in 1865. While much remains to be learned about exactly what made Smithsonian tick, Burleigh has provided a much richer sense of the social, political, and cultural context that produced him and the marvelous institution that bears his name.

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AFFAIRS WITH RELATIVES, WILD OR NOT

Dangerous Liaisons? When Cultivated Plants Mate with Their Wild Relatives. Norman C. Ellstrand. Johns Hopkins University Press, Baltimore, 2003. 268 pp. \$65.00 (ISBN 080187405X cloth).

In the fall of 2001, a paper in the journal *Nature* (Quist and Chapela 2001) reported genetic evidence that transgenes from genetically engineered (GE) maize had moved into traditional maize varieties (known as farmers' varieties, or FVs) in relatively remote areas of the southern Mexican state of Oaxaca. This was big news for a number of reasons: Oaxaca lies in the region of maize domestication and diversity and within the home range of maize wild relatives (teosintes); Mexico

had imposed a moratorium on the planting of GE crops in 1998; maize is the staple food and primary crop of most of Mexico's rural communities, especially the indigenous ones that dominate Oaxaca; and finally, the global debate about GE plants was continuing to escalate. That report and its repercussions have their own story, which continues to unfold.

In a broader sense, the 2001 report and the ensuing debate raised many fundamental questions, the answers to which remain hotly contested: Will the transgenes persist? What does it mean? Will teosinte or FVs be endangered? It also catapulted seemingly obscure areas of biological research of primarily academic interest—such as gene flow in plants—into the thick of heated, headline debates. Norman Ellstrand, professor of genetics and director of the Biotechnology Impacts Center at the University of California–Riverside, has been a leader in this research for nearly 20 years.

In *Dangerous Liaisons? When Cultivated Plants Mate with Their Wild Relatives*, Ellstrand walks us through a careful consideration of the population genetic evidence on this subject and discusses some of the implications for the case of transgenic crop varieties and their interbreeding wild relatives.

The chapters (1–4) of part 1 prepare readers for the journey into the subject of plant gene flow, with explanations of terms, processes, and theories about seed and pollen movement, hybridization, and introgression. In part 2 (chapters 5–8), empirical studies clarify theory and in many cases demonstrate the need to reexamine our assumptions about spontaneous hybridization between crops and their wild relatives. In an update and extension of an earlier paper (Ellstrand et al. 1999), Ellstrand reviews evidence for hybridization with wild relatives for all but three of the 25 most extensively sown world crops (chapter 7), noting that hybridization occurs across plant mating systems, genera, and growing environments, and is the rule rather than the exception. Part 3 (chapters 9–12) considers the consequences and larger implications of crop–wild relative gene flow. Using both theory and empirical studies, Ellstrand offers informative exceptions to

common assumptions in discussions of gene flow in general and the potential risk of transgene movement in particular: for example, the possibility of persistence and evolutionary impact of locally detrimental immigrant alleles under certain circumstances; the lack of observed fitness cost of allelic complexes or transgenes when introgressed into wild relatives (e.g., herbicide resistance in wild *Helianthus* subspecies), including cases in which transgenes have provided an unintended fitness boost (e.g., larger flower size in *Arabidopsis thaliana*); and repeated flow of locally beneficial genes resulting in a net increase in wild relative diversity, depending on the number and diversity of gene sources (maize FVs to teosinte, sugar beet and chard and red beets to wild sea beets).

The final two chapters focus explicitly on transgenes. Chapter 11 considers how the effects of gene flow from transgenic versus conventional varieties to wild relatives might contrast, concluding that the two are not significantly different. However, in both cases there are some genotypes that, under certain circumstances, can have substantial negative ecological, agricultural, or social effects, some being especially troublesome (e.g., sea beet–sugar beet hybrids in the Mediterranean and Adriatic regions, stacking of herbicide resistance transgenes in weedy canola populations in Canada). The final chapter gives an overview of current approaches for containing transgenes to prevent the unlikely but possible problems that their movement into wild plant populations may create. Ecological management strategies (spatial and temporal isolation, barriers to pollen flow) place the burden of containment on farmers and are difficult to implement. Some forms of genetic management that are still under development—e.g., linking transgenes to tandem constructs that will be strongly selected against in the wild—seem most promising to Ellstrand.

Ellstrand encourages readers to take the long view of research findings, pointing out, for example, that although most studies thus far have found a net increase in genetic diversity in wild populations as a result of introgression of genes from

cultivated relatives, there are good reasons for caution because the situation may change. Some populations are not yet in equilibrium and gene frequencies may go to fixation, potentially resulting in a decrease or no change in diversity relative to pre-introgression levels.

A picture emerges of processes (inter-specific hybridization, introgression, persistence of immigrant alleles) and occasional consequences (evolutionary change, ecological and agricultural harm) that, while clearly not ubiquitous, still cannot be considered unusual on the basis of the evidence in hand. That this can at times have substantial consequences is well illustrated by the story that Ellstrand weaves throughout the book (chapters 1, 6, and 10) of hybridization between wild sea beets (*Beta vulgaris* subspecies *maritima*) and the interbreeding progenitor and weed of cultivated beets (*Beta vulgaris* subspecies *vulgaris*). This is the scientifically documented melodrama of what both researchers and practitioners considered to be an unlikely long-distance romance, including the substantial harm caused by the progeny of those encounters, and how their story was uncovered.

Overall, *Dangerous Liaisons?* provides a valuable evaluation and discussion of our knowledge of gene flow in plants and the implications for transgene movement into wild crop relatives, with great relevance for transgene flow into FVs as well. Ellstrand manages to infuse his discussion and explanations with both thoughtful caution—walking the fine line between the polarized sides of the transgene discussion by not venturing beyond what the data support or dismissing what lack of data cannot preclude—and the excitement of surprising new insights and the changes they demand of us. Visual presentations of the data and ideas discussed would have been a nice addition to the book (it contains only six figures and 13 tables). The book's accessible and informal style make it a pleasure to read, but that informality also makes the book's abrupt end without even a summary paragraph a bit of a surprise—why did our friendly companion in understanding plant gene

flow leave us without even a parting thought?

In Mexico and elsewhere, the discussion of transgenes and their flow into wild relatives of maize and Mexican FVs continues, including the current debate about lifting the 1998 moratorium on planting transgenic varieties for research purposes. The circumstances in Mexico raise questions concerning gene flow and containment that demand rethinking on the part of biologists and policymakers. For example, what will be the impact on genetic diversity in FVs, given what is known about their genetic structure in contrast to that of MVs (modern varieties) (see pp. 141, 181)? Lack of monitoring for primary or secondary ecological impacts is a concern in wild plant populations (p. 183), but who will monitor traditional agricultural systems for such impacts? Management of gene flow may be sought through linking transgenes to tandem constructs tailored to lower fitness in environments outside of industrial agricultural fields (p. 201), but how might those affect performance in the low-resource agricultural systems ubiquitous in Mexico and the “third world”? These are just some of the myriad questions about transgenes that will benefit from the understanding of gene flow and the approach to investigating it demonstrated by *Dangerous Liaisons?*

At one point in his discussion, Ellstrand comments that “thinking about impacts [of GE crops] involves thinking out of the box” (p. 164), and this book, as well as his own research on hybridization between cultivated and wild plants and the potential significance in the case of transgenes, opens the door for us to do just that.

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GETTING RIGOROUS ABOUT DEVELOPMENTAL INSTABILITY

Developmental Instability: Causes and Consequences. Michal Polak, ed. Oxford University Press, New York, 2003. 488 pp., illus. (ISBN 0195143450).

The term “developmental instability” (DI) refers to the inherent degree of variability or “noisiness” of biological development. DI cannot be observed directly, but its occurrence is signaled by the phenotypic variability of comparable structures whose development took place under presumably identical internal (genetic) and external (environmental) conditions. The greater the divergence of such structures from one another, the greater the inferred degree of DI.

The phenomenon of DI was first identified and defined a century ago, in work on plants, by the eminent biometrician Karl Pearson. Forty to 50 years later, its investigation received impetus from some critical work and thinking by a small group of biologists, in particular C. H. Waddington, Kenneth Mather, and John H. Thoday. Nevertheless, it remained a rather neglected subject until the mid to late 1980s, when it experienced a surge of interest, becoming a fashionable subject in the 1990s. Yet despite this long history of attention and analysis, the precise significance of DI in the biology of complex organisms and for its investigators has remained frustratingly elusive. Perhaps the only point of universal agreement is that the phenomenon of DI is of interest and significance.

The particular focus of attention for the past 20 years or so has been the proposition that there should be an inverse relationship between DI and fitness; the greater the DI, the less fit the animal or plant will be. Another related

idea, associated initially with Therese Markow and Anders Pape Møller, in particular, is that the visible morphological asymmetries that develop as a result of DI serve as scorable indicators of (poor) fitness, and these asymmetries reduce the probability of successful mating. In effect, this hypothesis links DI to another idea that was becoming fashionable in the 1980s after a similarly long period of neglect, namely, Darwin's idea of sexual selection. The idea has a corollary: If the effects of DI are signaled to potential mates, as this hypothesis suggests, then there should be selection for "good genes" that reduce DI in general and the corresponding visible asymmetries produced by it.

Crucial to testing this hypothesis is the way in which one measures DI, since it cannot be detected directly by simple observation. The necessity of comparing structures with identical genotypes means that for sexually reproducing organisms, one has to compare identical structures arising within the same individual. For individual animals, the simplest measure is deviations from perfectly symmetrical left and right structures, such deviations being termed "fluctuating asymmetry" (FA). The critical assumptions in using FA as a surrogate for DI are that the left and right sides of the developing animal experience identical environments during development and that they are wholly independent of each other. Estimates of the variance of difference within a population, in principle, yield estimates of FA and, hence, the degree of underlying developmental instability. One problem with FA as a measure of DI, however, is that it has only one degree of freedom. To measure variances accurately under these conditions requires accurate measurement both of (often) small differences and of large sample sizes. For plants, measures of departures from symmetry are easier because one can compare multiple structures, such as flowers, leaves, or seeds, that should in principle be identical in the absence of DI.

The multiauthor volume under review here, edited by Michal Polak (University of Cincinnati), examines the subject in depth. It has two broad aims.

The first is to provide a picture of what one can currently conclude about DI in terms of its genetic and biological bases, its significance in development, and its importance for evolution. The second, and no less important, aim is to examine the methodological problems inherent in the quantitative assessment of DI in actual populations and to arrive at some degree of consensus on the best analytical approaches.

The book consists of 24 chapters. The list of contributors includes all, or nearly all, of the best-known figures in the field, plus many of the field's key younger scientists. The chapters are grouped into five sets devoted to (1) the developmental origins of DI (six chapters), (2) the genetic foundations of DI (five chapters), (3) the fitness consequences of DI (five chapters), (4) the statistical tools used to measure DI (three chapters), and (5) studies on environmental stress and its applications (five chapters). Partitioning the subject in this way is both sensible and

helpful but, as one might expect, there are overlaps in discussion between the different sections. For instance, some discussion of the genetic foundations of DI (section 2) creeps into several of the chapters on development (section 1), while it is impossible to discuss the genetic causes of DI (section 2) without first discussing some aspects of the developmental processes themselves.

Space does not permit a detailed accounting of the individual chapters, but it seems safe to predict that, regardless of one's particular area of interest in DI, the reader will find much of interest. For this reviewer, the key chapters were the first two and the final one. The former deal with developmental perspectives on the sources of DI and were written, respectively, by H. F. Nijhout and G. Davidowitz and by Christian Peter Klingenberg. The final chapter in the book, also by Klingenberg, deals with the uses of FA to ascertain the degree of dependence between developmental

modules, a novel and interesting application of the ideas. I also found the historical perspective written by Charles M. Woolf and Therese A. Markow on the differing historical views that informed the concept of "developmental homeostasis" quite valuable. For the statistically minded reader, on the other hand, several of the chapters in sections 3 (fitness consequences) and 4 (statistical tools) will undoubtedly have the strongest appeal. (Correspondingly, for the relatively statistically unsophisticated, those chapters will surely be hard going.) Finally, for those readers who principally want to find out about the uses of FA as a measure of "stressors" in the environment, the chapters in the final section will be of strongest interest.

Despite the inevitable differences of perspective presented in a multiauthor book, one gets the sense that there is growing agreement about certain issues. For example, it becomes evident at least halfway through the book that there is a consensus that much of the work carried out in the 1980s and 1990s, which initially supported the sexual selection connection, was not robust. Several of the chapters (in sections 3 and 4) grapple with the methodological, analytic, and statistical problems that may have led to a premature acceptance of the idea that FA is an important signaler in sexual selection. (And there are some interesting discussions of just why the earlier work seemed to provide such initial strong support for the idea.)

A second area of general, if not complete, agreement is that the FA estimates for different traits are usually not highly correlated. Just why this might be so is explicable in terms of a hypothesis published several years ago (Christian Peter Klingenberg and H. Frederik Nijhout, "Genetics of Fluctuating Asymmetry: A Developmental Model of Developmental Instability, *Evolution* 53 [1999]: 358–375). This model predicts that there are no general "FA genes" but that the FA for any trait is based on the specific genetic foundations of that trait. If this is the case, then the "good genes" hypothesis of sexual selection—involving the use of FA by animals as a signaling device for the possession of such genes—is in trouble.

Indeed, one gets the sense that as the tests for FA have become more rigorous with time, there has been declining support for this hypothesis.

Altogether, the book is a pleasure to read. The individual chapters are well written and the book as a whole has clearly been well edited. It is also handsomely produced, with good clear print, decent figures, and very few typographical errors. It is, of course, impossible to predict what its shelf life will be. New findings of interest continue to arise. For instance, a new analysis (James R. Kellner and Ross A. Alford, "The Ontogeny of Fluctuating Asymmetry," *American Naturalist* 161 [2003]: 931–947) suggests that during development, FA becomes less pronounced, indicating that left and right sides *do* communicate in some manner during development to achieve a degree of developmental matching. If confirmed, this finding undermines a key assumption in the use of FA as a measure of DI. As other new findings are made, some are bound to require reevaluation of current ideas, rendering some of the material here obsolete. Yet my guess is that a fair number of the chapters will continue to be of value 5 to 10 years from now, and a few of them, such as the historical perspective that Woolf and Markow provide, will remain of interest even longer. For anyone working on developmental instability or related subjects, this book is to be highly commended. It is an invaluable resource for the field and may be such for some time to come.

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NEW TITLES

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