

DESCENDED FROM DARWIN
INSIGHTS INTO THE HISTORY OF
EVOLUTIONARY STUDIES, 1900–1970

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American Philosophical Society
Philadelphia • 2009

TRANSACTIONS
of the
AMERICAN PHILOSOPHICAL SOCIETY
Held at Philadelphia
For Promoting Useful Knowledge
Volume 99, Part 1

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ISBN: 978-1-60618-991-7

US ISSN: 0065-9746

Library of Congress Cataloging-in-Publication Data is available from the Library of Congress.

CHAPTER 10

NATURAL SELECTION IN THE FIELD

INSECTICIDE RESISTANCE, ECONOMIC ENTOMOLOGY, AND THE EVOLUTIONARY SYNTHESIS, 1914–1951

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INTRODUCTION

In his 1937 book, *Genetics and the Origin of Species*, Theodosius Dobzhansky cited the emergence of insect populations that were resistant to chemical insecticides as “probably the best proof of the effectiveness of natural selection yet obtained” (Dobzhansky, 1937, p. 161). Dobzhansky learned of insect resistance first-hand from Henry J. Quayle, an economic entomologist and director of the Citrus Experiment Station in Riverside, California (Perkins, 1982, p. 65). Although by the mid-1930s, there were more than two dozen scientific articles published on insecticide resistance, Dobzhansky simply noted that Quayle “permits me to quote the following data from his manuscript” describing several species of insect pests, known collectively as scales, found in the citrus groves of southern California that no longer could be controlled by the standard chemical treatment of hydrocyanic gas fumigation. Dobzhansky further noted that “careful laboratory experiments have established beyond a reasonable doubt that the difference between the cyanide-resistant and the non-resistant strains is a real one,” by which he meant that the cause was due to genetic variation in the insect populations (Dobzhansky, 1937, p. 161).

The examples of insect resistance found in natural populations of citrus scale in southern California provided a key piece of evidence in the formulation of Dobzhansky’s “synthetic” theory of evolution. In the subsequent editions of *Genetics and the Origin of Species* published in 1941 and 1951, he greatly expanded the section on historical changes of natural populations in which he discussed insect resistance, eliminating some of the outdated references to industrial melanism and crab body size that

formed the bulk of his evidence for selection in the 1937 edition. He also included newer field and laboratory studies on resistance to insecticides, as well as the related phenomena of phage-resistance in bacteria.

Quayle and his group at the Citrus Experiment Station were not the first to study insect resistance to insecticides. In 1897, an entomologist from the New Jersey Agricultural Experiment Station noted the appearance of insect strains in Colorado and the eastern United States that no longer responded to standard treatment by kerosene spraying (Smith, 1897). In 1914, Axel L. Melander, an economic entomologist from Washington state described difficulties controlling the San Jose scale, a common apple orchard pest, dating back to 1908 (Melander, 1914). By the early 1940s, field researchers had identified about ten agricultural pests and laboratory strains that were capable of withstanding exposures to insecticides that had previously been highly effective in killing these same species (Quayle, 1943). All of these cases involved resistance to inorganic insecticides such as those based on lead, arsenic, cyanide, and other toxic compounds that had been in use since the nineteenth century. In addition, each of these early cases of insect resistance was a relatively local occurrence.

The phenomenon of insect resistance to insecticides achieved international scope in the mid-1940s following the introduction and widespread use of DDT and other organic insecticides that transformed insect resistance to a global agricultural and public health dilemma (Ceccatti, 2004a; Simon, 1999). By the early 1950s, there were more than two dozen resistant insect species—from houseflies and mosquitoes to granary weevils and bedbugs (Babers & Pratt, 1951). With the widespread application of DDT and other synthetic organic insecticides following the Second World War, insecticide resistance became not only a concern for agriculture but also a worry for global public health and even the military. At a 1951 conference convened by the U.S. Army Medical Research and Development Board, A. D. Ness, the Assistant Chief of the U.S. Public Health Service, noted that “insecticide resistance is not a new problem to the agricultural entomologist, but to the medical entomologist it is a relatively new problem. It did not become important until the so-called DDT era, starting with . . . the development of resistance by the louse *Pediculus*, discovered in Italy in 1947, and the resistance of houseflies developed in most parts of the world where there has been wide-scale application of DDT” (National Research Council, 1952, p. 1).

Nevertheless, in the decades prior to the introduction of DDT, insect resistance to insecticides posed significant economic problems in the affected areas and also challenged scientists, notably entomologists working at agricultural research stations, to provide a coherent scientific explanation of the phenomenon and to develop practical solutions. As will be discussed in this chapter, a small group of American scientists working on resistance in the 1920s and 1930s drew on available biological knowledge of genetics and physiology to offer explanations of resistance but were not able to provide a general theory to explain the phenomenon. Dobzhansky provided such an explanatory framework in the 1937 book and the new “synthetic” view of evolutionary theory gradually gained ground among economic entomologists in the 1940s beginning with Quayle and his colleagues in Riverside. Yet situating insect resistance within the prevailing genetic-evolutionary schema of variation and selection did not immediately provide a practical solution to the problem of resistance in the field.¹ Resistance research into the 1940s continued as it had since the 1910s by, first, documenting individual cases of resistance and, second, by postulating biological mechanisms to account

for the phenomenon. During this time period, strategies for dealing with insect resistance were limited to finding alternative chemical compounds that were effective in controlling resistant strains. In a 1949 review of the subject, a USDA entomologist concluded that “sufficient evidence has not yet been accumulated to permit postulation of a theory as to the cause of the phenomenon” (Babers, 1949, p. 21).

Historians of biology have typically portrayed Dobzhansky’s role in the evolutionary synthesis as a conduit or bridge between what had been up to then two distinct research communities, naturalists and geneticists, the former focused primarily on describing species in nature while the latter centered on laboratory experiments.² But insecticide resistance research from the 1910s to the early 1940s shows other aspects of the biological community that have not received as much historical attention, but that also played a part in larger developments of genetics and evolutionary biology during the synthesis period. One group consists primarily of economic entomologists working at state agricultural research stations and at the federal level for the USDA’s Bureau of Entomology.³ Another important group of biological researchers were located in industrial research laboratories of chemical companies producing insecticides.⁴ Although in the pre-World War II period, the locus of insecticide resistance research was predominantly at agricultural research stations in the United States, the flow of information and research personnel between the field stations and university and industry research laboratories was significant and dramatically increased after the war as insecticide resistance became a more global agricultural and public health concern.

INSECTICIDE RESISTANCE RESEARCH, 1914–1937

The earliest published report of insect resistance to insecticides was by John B. Smith, an economic entomologist at the New Jersey Agricultural Experiment Station in a short notice in *Garden and Forest* in 1897. Smith noted that some entomologists had observed variations in the effectiveness of certain chemical treatments on insects in different localities. “Insects that succumb readily to kerosene in the Atlantic states,” he explained, “defy it absolutely in Colorado [and] washes that easily destroy the San José scale in California are ridiculously ineffective in the Atlantic states.” Smith cited these examples of variability in susceptibility to chemical treatments among natural populations to advance his argument for the continued study of insects in the field even after their life cycles had been demonstrated. Many entomologists, he argued, assumed that once the life history had been studied, it was not necessary to carry out additional investigations since the insects were assumed to be constant from place to place. But, Smith explained, “observations carried on during the course of the experiments also indicated an altogether unexpected amount of variation from the published histories of many species, and an astounding difference in the amount of resistance to poisons, either external or internal.” Smith also noted several “contradictory results” in the published literature that would “seem to demonstrate the necessity of studying each destructive species in each distinctive environment.” Smith used this reference to insect resistance to challenge his colleagues to shift from their belief that species remained fixed over time and he urged other economic entomologists to reconsider this assumption and begin to study the geographic variability and temporal changes in insect populations (Smith, 1897).

Smith's admonitions went largely unnoticed (and unheeded) at the time but, in the first decades of the twentieth century, economic entomologists became aware of additional cases of resistant insects and began to investigate their causes.⁵ As early as 1908, economic entomologists received reports of resistant San José scale, an apple orchard pest, in Washington state. By 1916, researchers confirmed cases of resistant scale insects in the orange groves of southern California and by 1928 resistant codling moths, another apple pest, were sighted in Virginia. By 1950, more than a dozen species of agriculturally important insects had been identified, in addition to several laboratory-reared species (Babers, 1949; Babers & Pratt, 1951). The research approaches during this initial period centered on field observation and confirmation of the phenomenon, as well as laboratory studies focused on standardization of organisms, apparatus, and practices. The small group of scientists engaged in resistance research prior to 1940 consisted primarily of economic entomologists working at state-run agricultural research stations along with a much smaller number working at universities, in industry, and for the U.S. Department of Agriculture. For the most part, these researchers moved easily from field to laboratory and back again, testing field observations under more controlled laboratory settings and bringing laboratory knowledge to the field and farmer for final confirmation. As such, they can be classified under the rubric of what Robert Kohler has termed "border biology" (Kohler, 2002, pp. 1–6, 293–308). Yet, resistance researchers inhabited more than just the space between experimental laboratory science and natural history described by Kohler. Many of them also felt at home in the very different cultures of the agricultural field station, university, and corporation—each of which often had its own laboratory and field setting.⁶

RESISTANCE RESEARCH IN THE FIELD

In 1914, Axel L. Melander from the Washington State Agricultural Research Station published a report asking, "Can insects become resistant to sprays?" and two years later Henry J. Quayle of the Citrus Experiment Station in Riverside, CA, inquired, "Are scales becoming resistant to fumigation?" The fact that these two titles were framed as questions indicates a degree of uncertainty about the nature of the phenomenon of insect resistance at the outset, despite its increasing prevalence in fruit-growing regions along the West Coast.

In his first article, Melander noted that he had confirmed earlier reports from the Clarkson Valley region of Washington state that a significant portion of the San José scale survived the standard treatment of sulfur-lime there, even when applied at increased concentrations, while the scale pest in other regions could be controlled with the standard amount. This observation, he described, led him to conduct a series of experiments that confirmed the earlier observations. At some locations there was a complete killing of the scale with the typical sulfur-lime concentrations, but the Clarkston site had a significant percentage still living after several weeks. As a control, scales treated with oil emulsions were capable of complete control in all locations including the Clarkston Valley, indicating the scales had a specific response to the sulfur-lime compound. "It is evident from these figures," Melander concluded, "that the San José scale at Clarkston manifests a decided resistance to the action of sulfur-lime" (Melander, 1914, p. 169).

But what was responsible for this resistance? Melander reviewed several possible explanations culled from recent reports of organisms adapting to an otherwise inhospitable environment. Many organisms, he noted, had become “acclimatized” to harsh environments such as sulfur and thermal springs, hypertonic salt concentrations, and alkaline lakes, although Melander does not cite specific mechanisms in these cases. Alternatively, the San José scale might be becoming “progressively resistant” to the gradual application of sulfur-lime wash as had been demonstrated by recent work on gypsy moths and arsenic spray. But, Melander noted, this was a case of “an adaptation of the individual only” and it was not known how the “acquired immunity” and “arsenic antibodies” could be transmitted to subsequent generations. Melander further noted that “the physiological effect of sulfur-lime is believed to be due to a chemical reduction of the insect” although he does not provide more details about this proposed mechanism of action. Without more definite knowledge about the physiological mechanisms involved, Melander concluded that the resistance of the San José scale to sulfur-lime wash was hereditary since his observations had indicated that there was a “sex-difference, for among the resistant individuals escaping the action of the spray, the majority are males” (Melander, 1914, pp. 170–171).

After this brief discussion of possible physiological or genetic explanations, Melander quickly returned to the pragmatic concerns of his constituent apple-growers. “What is the economic importance of the appearance in a locality of a resistant strain of the San José scale?” he asked. In response, Melander drew on current genetic theory as a way to bring calm to a potentially drastic situation. “An alarmist might say that a few such scales would soon result in a totally immune insect, brought about by annual spraying. But viewed from a Mendelian standpoint,” he assured, “the consequences are less direful.” Melander admitted that repeated sprayings could result in a “pure line” of resistant insects. But in practice, there were many individuals in the field that were subject to the spraying, hence there would still be a proportion of nonresistant individuals in the population as a whole. This led to the “strange assertion that the more faulty the spraying this year the easier it will be to control the scale the next year” (Melander, 1914, p. 171).

The following year, Melander published a second report in which he warned that the resistant scale insects were “becoming increasingly prevalent in some of the older fruit sections of Washington” and that further research has shown that “not only are the scales slow to succumb to the effects of sulfur-lime but that there is a pronounced and great individual difference, many scales manifesting even a complete immunity to this insecticide.” Furthermore, he noted that “one cannot agree with the statement that the prevalence of the insect is due to faulty application. It must be due in part at least in these cases to an inherent vigor of the insect to withstand the toxic effects of the spray” (Melander, 1915, pp. 475–476).

Melander drew several conclusions from these and subsequent studies. He noted that there was a great variation in susceptibility of individual scales to sulfur sprays and that the amount of tolerance also varied by location. He attributed the resistance to a “natural vigor” displayed in some populations and not in others and discounted the role of external factors such as weather, spraying technique, parasites, or the conditions of the host plants. But Melander could not definitively say that the resistance was heritable. Since spraying was conducted only once per year during which time the scale went through about ten generations, direct hereditary effects could not be seen.

Any genetic selection for resistance, he reasoned, would be lost in the intervening generations between sprays. Alternatively, the increased tolerance of scales to spraying could be due to “acclimatization to lime-sulfur [as] an annual acquirement, [and] not necessarily heritable” (Melander, 1923, p. 47).

The other early example of insect resistance to insecticides came from southern California where entomologists at the Citrus Experiment Station (CES) in Riverside observed the resistance of the citrus red scale to hydrocyanic acid (HCN) fumigation. As Henry J. Quayle, the director of the station, later noted, evidence of “unsatisfactory results of fumigation” near Corona, CA, first emerged by 1915. Subsequent fumigation experiments conducted at the CES, “together with that of several different commercial firms, led us to suspect that the red scale is actually more difficult to kill in that district [Corona], rather than to ascribe the poor results to insufficient dosage, leaky tents, or lack of attention to the details of the work” (Quayle, 1922, pp. 400–401).

In 1922, Quayle reported on a series of experiments comparing the effects of fumigation for red scale at six locations in southern California. In each of these experiments, scales from the Corona district displayed a markedly higher degree of survival—ranging from 5- to 45-fold—after fumigation than in other areas, with increased resistance. Quayle also tested the effects of the weather and the condition of the trees being sprayed (such as the amount of foliage present) and found that, although these factors did have some effect on the effectiveness of the fumigation, it was not enough to account for the observed degrees of resistance. These experiments, Quayle concluded, provided the proof of insect resistance that was missing from the earlier field tests and observations. “In the case of the red scale at Corona,” he wrote, “definitive proof of resistance was lacking until comparative tests were made in which the variable factors of time and place were eliminated. At this time, however, after seven years’ experience, observation of experimental and commercial work in the field is sufficient to establish the fact of resistance” (Quayle, 1922, p. 403).

The situation in California was, therefore, similar to that in Washington State and the San José scale. Prolonged application of a specific chemical insecticide that typically killed the target insect eventually led to the emergence of a resistant or tolerant insect population. This resistance was specific to a single locality; insects in most other areas were still susceptible to the chemical treatment. Entomologists at the agricultural research stations subsequently conducted field experiments to confirm the resistance as a biological (genetic) phenomenon and to rule out the influence of external factors such as the weather or faulty application techniques.

LABORATORY STUDIES OF RESISTANCE

Following these initial reports and experimental field work on insect resistance in Washington state and southern California, economic entomologists in other states reported additional cases of insects that no longer succumbed to standard chemical treatments. At the same time, these observations and experiments in the field were accompanied by corroborative research in the laboratory.

In the mid-1920s, one of Quayle’s colleagues at the Citrus Experiment Station, A. M. Boyce, began a series of genetic investigations of insect resistance primarily using *Drosophila* but also laboratory strains of agriculturally important insects such as aphids, weevils, beetles, and scales. In these breeding experiments, Boyce set out

“to produce through continued artificial selection a strain of insects more resistant to HCN gas than were the original parents” (Boyce, 1928, p. 717). The selection of *Drosophila* for HCN resistance was moderately successful, resulting in offspring with up to 12% higher survival than the parental strain, but the high variability of the results led Boyce to conclude that the phenomenon of resistance had a more complicated basis than could be determined in these few investigations.

The third major case of insecticide resistance to be reported in the U.S. came from the apple orchards of Virginia. Beginning in 1928 and continuing into the 1940s, Walter Hough of the Virginia Agricultural Experiment Station conducted field and laboratory studies on a resistant strain of the codling moth larva, a common apple orchard pest, which he had obtained from Colorado. Compared with a Virginia strain of the insect, the Colorado codling moth demonstrated a six-fold greater ability to infest apples sprayed with the standard lead arsenate insecticide. In a later series of genetic experiments, Hough crossed the two strains together and found that the progeny’s ability to surmount the chemical treatment was midway between the two parent strains. Furthermore, backcrosses of these same intermediate progeny with either parental type gave offspring whose level of resistance had shifted in the direction of the parent type involved in the cross. In other words, codling moth resistance to lead arsenate had a demonstrable genetic component (Hough, 1934).

Another laboratory-based approach to the resistance question came from F. L. Campbell of Harvard University’s Bussey Institution, where Melander conducted his doctoral work. In the mid-1920s, Campbell attempted to induce an immunity or tolerance to poisons in silkworms reared on sub-lethal doses of an arsenic compound.⁷ Although the initial trials proved unsuccessful (primarily due to the relatively small number of insects tested), this type of study would serve as an experimental model for a wide variety of investigations beginning in the late 1940s.⁸

Much of this early research in both field and laboratory centered on identifying the genetic and physiological basis of resistance. Although this line of inquiry did much to confirm the biological basis of resistance, there was little consensus about the mechanisms involved. In fact, most of the experimental studies of resistance showed that different mechanisms were involved in each individual case—and no universal model or theory could be advanced.

INDUSTRY’S FIRST REACTION: RESISTANCE TO RESISTANCE

This lack of consensus about the underlying mechanisms of resistance allowed some to question the biological basis for insecticide resistance. There were also those who expressed skepticism about resistance as a biological—or at least a genetic—phenomenon and instead proposed that the increased ability of some insects to withstand insecticidal treatment was due to environmental factors such as temperature and humidity. Most of these studies came from researchers at chemical and fumigation companies, although the number of companies involved in resistance research in the 1920s and early 1930s was very small, perhaps only three.⁹

One such nonheritable alternative explanation was termed “protective stupefaction” and referred to the temporary effect of exposure to a low dose of insecticide that allowed the insect to withstand a higher dose at a later time. This kind of resistance was not transmitted from generation to generation and could even dissipate over time

in the same insect—hence it was not a fixed biological characteristic (although it could involve a physiological or biochemical mechanism).¹⁰

Another investigator who pursued nongenetic explanations of insect resistance was William Moore, who worked for Owl Fumigation Company in California and later for the American Cyanamid Company, based in New York. In 1933, Moore published his studies questioning resistance in California red scales in direct response to Quayle's work in Riverside. In a comprehensive series of field tests, Moore investigated the effects of a variety of external factors on the susceptibility of red scale to HCN fumigation, including the type of concentration, the developmental stage of the insect, the temperature of the host plant, and the ambient temperature and relative humidity before, during, and after the fumigation. Moore found that both HCN concentration and insect developmental stage had little effect on susceptibility to fumigation and that protective stupefaction "may or may not be an important factor." Instead, he concluded that both temperature and humidity "had a decided influence" on the effectiveness of HCN fumigation to kill red scale—regardless of the strain tested. Moore concluded, "the main difference between 'resistant' and 'non-resistant' red scale is the influence . . . of certain environmental conditions" and postulated that the varying climatic conditions in different localities may be responsible for the observed "resistance" (Moore, 1933, pp. 1160–1161; see also Moore, 1936).

STANDARDIZATION OF RESISTANCE

One byproduct of insecticide resistance research during the 1920s and 1930s was to standardize experimental organisms and methods. The work by Boyce and Hough, cited earlier, was among the first to develop uniform laboratory strains of resistant insects. Another aspect of standardization involved the apparatus and methods associated with testing new chemical compounds for their insecticidal activity. The impetus for standardized testing procedures and apparatus came primarily from industry and only gradually crossed the boundary to agricultural research stations and university laboratories.

In 1928, C. H. Peet and A. G. Grady, from Rohm & Haas, the Philadelphia-based chemical company, developed a set of procedures and related apparatus "in order that insecticidal tests may be made sufficiently simple to be carried out in any reasonably adequate laboratory and sufficiently uniform to be quite strictly comparable wherever they may be performed" (Peet & Grady, 1928, pp. 612–613). The Peet-Grady test, as it came to be known, was initially developed for testing potential insecticidal compounds, not initially to study resistance. The test consisted of a standard organism (typically the housefly), a standard testing apparatus to control for environmental variables, and a standard procedure for introducing the test compound and measuring its insecticidal effectiveness. Peet and Grady acknowledged the high degree of variability in any biological test but proposed that "the superficial variables which have heretofore been ignored, or too little considered, can be so accurately controlled that only the biological variable remains to remove such tests from strict reproducibility and the average will be just as certain as life insurance mortality tables" (Peet & Grady, 1928, p. 613).

The analogy to actuarial tables was not too far from the truth. The Peet-Grady test involved placing one or two hundred houseflies in a 6-foot cubic chamber (originally

made of wood painted with white enamel) and introducing a set amount of the test compound through small holes drilled into the ceiling using an atomizer coupled with a fan. After ten minutes, a small flap built into the chamber was opened to allow observation of the results. Flies still clinging to the walls were counted and considered to have survived the treatment, while those on the floor were collected in cages and observed for 24 hours to determine whether they recovered, in which case they were added to the number of survivors, or had been killed. These results were then translated into an “insecticidal coefficient” that quantified the compound’s effectiveness. “Tests conducted following this procedure,” Peet and Grady concluded, “show a low average variation and it is entirely reasonable to presume that any investigator could obtain very uniform results following this method” (Peet & Grady, 1928, p. 617).

In 1936, representatives of the National Association of Insecticide and Disinfectant Manufacturers formally adopted the Peet-Grady method to test new compounds for their insecticidal activity. The test gave manufacturers a simple metric based on the percentage of insects that were killed in the Peet-Grady chamber under standard conditions that could be used to compare results of a test compound to a standard preparation based on pyrethrum, called the Official Control Insecticide (O.C.I.) (Weed, 1936). Although the Peet-Grady test was not specifically designed to ascertain insect resistance to a particular compound, resistance was soon recognized as a limiting factor in the test that threatened its usefulness in industry. In 1937, Jared Ford of the Kilgore Development Corporation noted significant “inaccuracies” in Peet-Grady results due to “the wide variation in the resistance of the *individual* flies in the same group.”¹¹ Kilgore recommended treating any test group of insects as a variable population for which resistance could be described as a normal distribution curve, rather than assuming that all insects in the group had the same susceptibility to the test compound. He then developed a statistical adjustment for Peet-Grady results that related the direct measure of the percentage of insects killed in the chamber to a normal distribution curve in which most insects had some average level of resistance but a diminishing number were either more or less resistant following the twin tails of the curve. This adjustment “takes into account the variation in resistance of the individual flies and makes possible a direct comparison of any two or more insecticides which have been tested against the O.C.I. for the same year” (Ford, 1937, p. 119).

In addition to any improvements in testing that Ford’s recommendation brought, it was also significant in its relatively early recognition (and acceptance by fellow industrial chemists) of biological variation within natural populations. Among many biologists (and especially economic entomologists) the same concept would still be a hard sell into the 1950s. For example, in remarks presented (in absentia) to a 1951 conference on insecticide resistance attended by leading researchers in academia, government, and the military (but not from industry), Dobzhansky admonished “biologists [to] abandon the habit of thought, inherited from the pre-evolutionary era, which regards each species, race, or population as an embodiment of a certain ‘type’ or ‘norm.’”¹²

INSECTICIDE RESISTANCE AND DOBZHANSKY’S *Genetics and the Origin of Species*

Genetics and the Origin of Species was based on a series of lectures Dobzhansky delivered at Columbia University in the fall of 1936 and is widely viewed as one of the

first influential attempts to unify the findings of classical genetics with evolutionary theory, a movement that came to be known as the evolutionary synthesis.¹³ Dobzhansky himself described the book as a “discussion of the mechanism of species formation in terms of the known facts and theories of genetics” (Dobzhansky, 1937, p. xi). Although the revised editions incorporated newer field observations, laboratory research, and developments in theory, the basic argument of the book remained the same: genetic mutation and chromosomal rearrangements provided genetic diversity within populations; the competing forces of isolation and migration altered the genetic makeup of sub-populations; and natural selection culled unfavorable mutations and enhanced those that provided adaptive values of the species. But Dobzhansky did not view selection as a tertiary force designed for minor adjustments. Indeed, he argued that “natural selection is probably most important when the environment undergoes changes, for it is the sole known mechanism capable of producing a reconstruction of the genetic make-up of the species population from the existing elements” (Dobzhansky, 1937, p. 186).

Despite this central role for selection in the evolutionary synthesis, Dobzhansky acknowledged in the first edition that theory was outpacing experimental evidence for selection in the field. He admitted the “inadequacy of the experimental foundations of the theory of natural selection” although he noted that “the work to date has been concentrated mainly on proving the reality of natural selection as a process actually going on in wild populations, and a fair degree of success has been achieved in this field” (Dobzhansky, 1937, p. 176). This sentiment remained in the second edition of 1941, but was less evident, if not eliminated altogether, in the significantly revised third edition in 1951, which incorporated many laboratory and field studies that supported natural selection. Despite this growing body of evidence for natural selection, Dobzhansky continued to stress the importance of insecticide-resistant insect strains, although in the later editions he modified his 1937 claim that resistance was “the best proof of the effectiveness of natural selection” with the assertion that the cases of resistance “unmistakably owed their origin to natural selection” (Dobzhansky, 1941, p. 190; 1951, p. 94).

Dobzhansky discussed insecticide resistance in a section titled “Historical Changes in the Composition of Populations,” which he explained as instances “where a change in the genetic composition of a free living population has been observed to take place within historical time” (Dobzhansky, 1937, p. 159). In the first edition, he adduced three such cases but dropped two of these in the subsequent editions, leaving only insect resistance to bolster the claim that natural selection could be observed in the field, to which he added in the 1941 edition a related instance of resistance of a strain of wheat that was resistant to a common rust.¹⁴

As noted above, Dobzhansky’s knowledge of insecticide resistance came from a personal communication with Quayle at the Citrus Experiment Station in Riverside citing results that Quayle published in 1938. Although no evidence could be identified to substantiate a personal meeting or correspondence, it is likely, as Perkins notes, that Dobzhansky met Quayle either while he was preparing the lectures at Columbia, which he delivered in October and early November of 1936, or during the writing of the book manuscript in the winter of 1936–1937 (Perkins, 1982, p. 35). It is possible that the two researchers had communicated about insecticide resistance much earlier (Dobzhansky arrived in Pasadena along with the Morgan group in 1928), but

it seems more plausible that Dobzhansky learned about insecticide resistance shortly before or while he was preparing either the lectures or the book manuscript, since he initially cites personal communication with Quayle and does not cite earlier articles by Quayle or the other researchers such as Melander, Boyce, or Hough, who were already actively engaged in resistance research.

Regardless of these details, Dobzhansky's acquaintance with Quayle provided him with an ideal example of natural selection that combined field study with laboratory experiment.¹⁵ Already in 1937, Quayle and his colleagues had documented three separate cases of scale insects that survived previously lethal dosages of hydrocyanic acid fumigation. In addition, Dobzhansky noted that "careful laboratory experiments have established beyond a reasonable doubt that the difference between the cyanid-resistant and the non-resistant strains is a real one" (Dobzhansky, 1937, p. 161). Although not explicitly mentioned, the laboratory experiments were likely those conducted by Boyce, a colleague of Quayle's at the Citrus Experiment Station.

In the 1941 edition, Dobzhansky expanded his discussion of insecticide resistance to include not only Quayle's published findings, along with an illustration from his now-published paper, but also corroborative genetic work by some of Quayle's colleagues indicating that hydrocyanic acid resistance in the California citrus scale was due to a single sex-linked gene whose frequency in the population was dependent on the intensity of fumigation, that is, on the selective pressure in the environment (Dobzhansky, 1941, pp. 190–192).

By the time that the third edition of *Genetics and the Origin of Species* appeared in 1951, insecticide resistance had reached a heightened level of concern with the appearance of DDT-resistant houseflies and other threats to public health. Although these cases were not a surprise to Dobzhansky since they represented further examples of what had been observed earlier, he did, however, note two implications of insecticide resistance that were not immediately obvious to other researchers. First, insecticide resistance was similar to recent cases of antibiotic resistance in bacteria. Second, the strategy of chemical control "once considered satisfactory may no longer suffice, because the pests to be controlled undergo changes themselves" (Dobzhansky, 1951, p. 96).

RESISTANCE RESEARCH IN THE ERA OF THE EVOLUTIONARY SYNTHESIS, 1937–1951

The impact of Dobzhansky's book among geneticists and evolutionary biologists working in university settings has been well documented.¹⁶ Among practicing economic entomologists working at agricultural research stations the book's influence during the 1940s and early 1950s was greatest among the relatively small group of researchers focused on the resistance question. This group primarily consisted of Quayle and his colleagues at the Citrus Experiment Station in Riverside, CA, but also included scientists at the U.S. Department of Agriculture's Bureau of Entomology, who had been engaged in resistance research since the 1930s.

Among the larger community of economic entomologists, however, the implications of Dobzhansky's theory, especially what has been called his "population thinking," were not immediately evident, at least through the 1940s. Like many biologists in other fields of research, economic entomologists generally held a view of species

as fixed entities and much of the focus of Quayle and others in the years immediately following the publication of *Genetics and the Origin of Species* was to convince the larger entomological community of the significance of Dobzhansky's theory for their research. The phenomenon of insecticide resistance, since it was a recognized problem among economic entomologists, became a useful way to introduce the concepts of the evolutionary synthesis to these field scientists.

One person who was instrumental in the dissemination of Dobzhansky's ideas among economic entomologists was Harry S. Smith, a colleague of Quayle's in Riverside and president of the American Association of Economic Entomologists. Smith did not work directly on the resistance question but he was an outspoken proponent of biological alternatives to chemical insecticides and, therefore, very interested in the potential problems associated with the chemical approach to pest management. Smith and Dobzhansky also knew each other personally. In the second edition of *Genetics and the Origin of Species*, Dobzhansky cited a conversation with Smith, noting that the emergence of resistant strains of insect might indicate a misconception in the widespread use of chemical insecticides, although Dobzhansky refrained from endorsing a biological approach (Dobzhansky, 1941, p. 192).

The interaction with Dobzhansky did, however, influence Smith's own biological thinking and he actively sought to inform his colleagues of the significant implications of the evolutionary synthesis. In his 1940 presidential address to the American Association of Economic Entomologists, Smith noted that many field entomologists still regarded "the possibility that an insect species might materially change its habits within the lifetime of an individual entomologist . . . with a great deal of skepticism" (Smith, 1941, p. 1). This sentiment echoed the observation made by another Smith—John B. Smith of the New Jersey Agricultural Research Station who, as noted above, was the first to report insect resistance—more than 40 years earlier that entomologists needed to expand their view of insect species to allow for adaptive change in the course of a few generations. In the early 1940s, Harry Smith could adduce the growing body of field observations of Melander, Quayle, Hough, and others held together by the conceptual framework provided by the theoretical heft of Dobzhansky's treatment, but withheld judgment about the ultimate nature of resistance. "Changes have occurred in the habits of several species of insect pests, which *appear* to be correlated with environmental changes brought about by agriculturalists in the pursuit of their calling," Smith explained. "If this apparent relation proves to be a fact, it is one of far reaching importance" (Smith, 1941, p. 1, italics in original).

Despite his hesitation about the causal relationships between insecticide use and the emergence of resistant insects, Smith had no doubt about the implications of such an occurrence, which underscored his own preference for biological rather than chemical methods of insect control. After noting "two striking cases" in which chemical treatments had become "largely ineffective," Smith surmised that "there is every reason to believe that this condition will develop with many other pests, and the economic entomologist can expect to be continually faced with the prospect that many of his recommendations will, in time, become of doubtful value" (Smith, 1941, p. 9). As alternatives to chemical control, Smith urged intensified and coordinated research into the use of parasites to control insect pests and the breeding of host plants capable of resisting insect attack. In the end, Smith did rely on Dobzhansky's work in demonstrating the genetic basis for local variation in insect populations (what

he and others at the time termed “racial segregation”) and he explicitly commended those geneticists such as Dobzhansky “who in very recent years have tended to leave the laboratory and go directly into the field for their data [and who] have approached the question [of resistance] from the evolutionary angle” (Smith, 1941, p. 3). Smith’s initial sympathies with those who were skeptical of the idea of species change was perhaps another example of interdisciplinary bridge-building between his constituency of economic entomologists and what he labeled as “geneticists,” who included both the laboratory experimentalists and field naturalists identified by Mayr, Allen, and others in their historical analyses of the evolutionary synthesis (Allen, 1994; Mayr & Provine, 1980).

For his part, Quayle employed Dobzhansky’s arguments to convince his fellow economic entomologists of the biological reality of insect resistance. In a pair of review articles published in 1938 and 1943, following the appearance of the first and second editions of *Genetics and the Origin of Species*, respectively, Quayle continued to cite Dobzhansky in his effort to press the case for the “fact of resistance” that he had first advanced in 1922 (Quayle, 1922, p. 403). In the 1938 article, Quayle’s argument was directed primarily towards a few “dissenting opinions” who continued to argue for external factors such as variable weather conditions or the faulty techniques of farm workers in applying the insecticides (Quayle, 1938, p. 183). As noted earlier, one of these dissenting opinions came from William Moore, the industry scientist, whose investigations of various conditions of hydrocyanic acid fumigation on California red scale indicated that temperature and humidity “had a decided effect” in the ability of the gas to kill the target insects when tested under both normal field conditions and in standardized “fumatoria” (Moore, 1933, 1936). In response, Quayle reiterated the evidence from both field and laboratory studies in which such non-genetic factors as weather, geographic location, and developmental stage had been excluded. This time he was able to refer to Dobzhansky’s work—and authority—in outlining an evolutionary mechanism for increased resistance. “The phenomenon of resistance probably appeared in the first instance through mutations, or because of the presence of a mixture of the resistant and nonresistant strains in the original infestations in the California orchards,” Quayle concluded. “Which of these explanations is correct will probably remain forever obscure, in the opinion of Dobzhansky” (Quayle, 1938, p. 207).

Five years later, Quayle again saw it necessary to make the case for insect resistance—first, as an uncontested fact of nature and, second, citing Dobzhansky, as the result of natural selection acting on genetic variation within a species. Quayle further noted that “there was sufficient experimental evidence to establish that fact [of resistance] in the case of seven species, and observation or circumstantial evidence tends to support such a contention in the case of some others” (Quayle, 1943, p. 493). As indicated above, this was very close to the argument that Quayle had made some 20 years earlier that “observation of experimental and commercial work in the field is sufficient to establish the fact of resistance” (Quayle, 1922, p. 403). Clearly, there was a certain amount of resistance among Quayle’s colleagues in the economic entomology community to the concept that natural species could adapt in response to extreme environmental modification whether from selective pressure or another cause. This community inertia can be seen in Harry Smith’s 1940 address and also in the persistence of counter-explanations such as Moore’s through the 1930s. But this resistance

among economic entomologists to evolutionary explanations of resistance seems to have given way, if only gradually and without additional experimental evidence, to the persistent admonitions of Quayle and Smith.¹⁷

CONCLUSIONS

Prior to the Second World War, the problem of insecticide resistance was a relatively local concern to economic entomologists working at state agricultural research stations, a very small number of scientists employed by insecticide companies, and of course to the farmers in the affected areas. Resistance research begun by Melander and Quayle in the 1910s and continued by other scientists working at state and, later, federal agricultural research stations into the 1930s and early 1940s, focused, first, on establishing the biological basis of resistance in the field by excluding environmental factors and, second, on elucidating the underlying cause (genetic, physiological, behavioral) for the resistance. This research drew from traditional field techniques such as collecting, counting, and identification, as well as from laboratory methods, such as controlled breeding and selection experiments. In most cases, both types of research were carried out in tandem by the same researchers or groups of researchers. At the heart of this research were some very practical questions: what was the nature of resistance, and how could this knowledge be used to overcome resistance or prevent its occurrence in the first place. From the beginning, resistance research drew on current biological knowledge in the burgeoning fields of genetics and physiology to explain resistance, but no overarching theory or model was advanced to offer a general solution.

This began to change in the 1940s for two main reasons that were initially unconnected but together provided resistance research with a new urgency and scope along with a theoretical framework that promised greater understanding, if not a general solution, to the resistance problem. The first event was the development and widespread application of a new category of insecticides—the synthetic organics—led by DDT. DDT's initial promise was its “broad spectrum” of activity (it killed a wide variety of insects), its low immediate toxicity to nontarget organisms, and its persistence, which made the compound the “miracle powder” and “benefactor of all humanity” according to advertisements from the mid-1940s.¹⁸ Of course, some of these same attributes contributed to the public controversy over DDT initiated, in part, by the publication of *Silent Spring* by Rachel Carson in 1962. While it is not within the scope of this article to discuss this important issue, it is worth noting that, in addition to the more widely known and debated issue of toxicity, Carson devoted an entire chapter to the problem of insecticide resistance, titled “Nature Fights Back.”¹⁹

The second turning point for insecticide resistance research came with the publication of *Genetics and the Origin of Species*. The influence of this book among academic biologists and of Dobzhansky's role in bringing together Darwinian evolutionary theory with the more laboratory-centered genetics of the Morgan-Mendelian lineage is well known.²⁰ The main purpose of this paper has been to shed some light on another set of influences that have not received adequate attention in the history of biology. It should be clear that the combined field and laboratory research of economic entomologists on the resistance question beginning the 1910s provided a key

piece of evidence in Dobzhansky's formulation of the synthetic theory of evolution as outlined in *Genetics and the Origin of Species*.

Although the details of Dobzhansky's encounter with Quayle, Smith, and others in the economic entomology community of southern California remain obscure, one aspect for this fruitful exchange can be attributed to what Kohler describes as "the turning point in evolutionary genetics . . . when drosophilists left the laboratory for the field and invented practical methods for doing experiments with large and diverse populations of wild flies" (Kohler, 1994, p. 251). Dobzhansky's peripatetic nature and his strong belief in "population thinking" have rightly been traced to his early training in Russia (Adams, 1968, 1970; Alexandrov, 1994; Kohler, 1994, pp. 250–293; Krementsov, 1994). His noted bridge-building between naturalists and experimentalists, Darwinians and Mendelians, has also been adequately demonstrated (see references in note 2).

Dobzhansky's ability and willingness to engage with another group of biologists—the economic entomologists at agricultural experiment stations—had a decided influence on this group as well, as evidenced in the comments by Quayle and Smith noted above. Dobzhansky's theoretical framework (along with subsequent work by other evolutionary biologists) gave resistance researchers a more solid conceptual foundation on which to develop their own explanations—and possible solutions—to the problem of resistance. The field and laboratory entomologists could reciprocate by adding their small empirical piece to the evolutionary puzzle.

ACKNOWLEDGMENTS

Support for this research has been provided by the Swiss National Science Foundation through grant number 1114-061585.00. The author would like to thank Prof. Christian Simon, Historical Seminar, University of Basel, for helpful comments on this chapter.

NOTES

1. Indeed, the problem of insect resistance for global agriculture and public health continues unabated to the present time, although the goal of this research has shifted over recent decades from control and management to monitoring, containment, and mitigation. See, for example, Casida and Quistad (1998).
2. See Allen (1994); Kohler (1994, chapter 8); Kohler (2002, pp. 296–298); Mayr (1982, p. 569); and Provine (1971, 1986);
3. Discussions of various aspects of the field of economic entomology can be found in Perkins (1982); Palladino (1996); Sawyer (1996); Sorensen (1995); Jones (1973); Stoll (1995); Buhs (2002); Jansen (1996); and Castonguay (1998–1999). Helpful studies of research at American agricultural research stations in the twentieth century include Kimmelman (1988) and Finlay (1988). A review of economic entomology at the U.S. Department of Agriculture can be found in Dunlap (1980), and a comparison between U.S. efforts at insect control and chemical warfare is discussed in Russell (2001).
4. Of the many studies of scientific research in the chemical industry, valuable sources include Reinhardt (2001); Homburg, Travis, & Schröter (1998); Busset, Rosenbusch, & Simon (1997); and Travis (1998).
5. Smith's 1897 article is not cited in the resistance literature until a 1951 review by two USDA entomologists, Babers & Pratt (1951).

6. The role of economic entomologists in chemical industry laboratories and field stations is explored in greater detail in Ceccatti (2004b).
7. Campbell, 1926. This research echoes an attempt in the mid-1910s by another Bussey Institution researcher, R. W. Glaser, who developed a strain of gypsy moth that could tolerate high doses of arsenic. See Melander (1914, p. 170).
8. The geneticist James F. Crow, for example, developed a laboratory system for selecting DDT-resistance in fruit flies beginning in 1949. See Crow (1951).
9. Industry affiliations for resistance researchers in the leading economic entomology journal include the California Cyanide Company, the Owl Fumigation Corporation (later acquired by American Cyanamid), and the Pacific R&H Chemical Corporation.
10. See, for example, Gray & Kirkpatrick (1929); and Pratt (1931).
11. Ford, 1937, p. 116. In a footnote, Ford differentiated this individual variation within a group from variation between different groups, or strains, of insects.
12. Dobzhansky in National Research Council (1952, p. 86).
13. For background on the extensive historical literature on the evolutionary synthesis, see Cain (1993); Mayr & Provine (1980); and Smocovitis (1996, chapters 3 and 5). For information specific to Dobzhansky's life, research, and role in the synthesis, see the essays in Adams (1994a). Perspectives on Dobzhansky's work from fellow scientists can be found in Levine (1995).
14. The other cases were Weldon's 1899 observation that crab size had diminished in response to increased silt content of the water in certain localities and cases of industrial melanism noted in England, Germany, and elsewhere. In the second and third editions, Dobzhansky also mentions cases of geographical variation that were included in another section in the first edition.
15. See Allen (1994); and Kohler (1994, chapter 8), on Dobzhansky's penchant for combining field and laboratory biology.
16. Cain (1993, pp. 9–10); Adams (1994b, pp. 3–9). See also the essays in Adams (1994a) and Levine (1995).
17. Bibliographical research did not reveal additional articles by Moore or the other critics of genetic explanations for resistance following the publication of *Genetics and the Origin of Species* in 1937 and Quayle's description of its arguments in 1938.
18. Simon (1999, pp. 49–66); advertisements reprinted as figures 55 and 66.
19. Carson (1962, pp. 245–262). For a discussion of Rachel Carson's work and the debate over insecticides that followed the publication of *Silent Spring*, see Lear (1997); Russell (1999); and Simon (1999, pp. 138–168).
20. See, for example, Smocovitis (1996, pp. 20–21); Provine (1994, pp. 112–113); and Allen (1994, pp. 94–97).

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