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1914–2004

A Biographical Memoir by
ALAN R. TEMPLETON

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Hampton Lawrence Carson

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November 5, 1914–December 19, 2004

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HAMPTON ("HAMP") LAWRENCE CARSON made wide-ranging contributions to cytogenetics, evolutionary genetics, and the study of speciation. He was a pioneer at using cytogenetic analysis of chromosomal inversion patterns to study migration, local adaptation, and speciation in *Drosophila* and other insects. Hamp was an extraordinarily observant naturalist whose work on evolutionary genetics often led to unanticipated discoveries, such as his discovery that some species of *Drosophila* use the external nephric grooves of land crabs as a larval habitat. He had a remarkable ability to synthesize his observations into general theories to yield a deep understanding of the mechanisms of evolution.

Hamp's synthetic abilities are most apparent in his research on the Hawaiian *Drosophila,* perhaps his most widely known work. The pattern of evolution that he observed in Hawaiian *Drosophila* suggested to Hamp that founder events, perhaps just a single gravid female going from an older island to a younger one, could play a critical role in the origin of new species. This work on Hawaiian *Drosophila* and their adaptations to island ecosystems was honored by the awarding of the Joseph Leidy Medal by the Academy of Natural Sciences in Philadelphia in 1985. Of his many honors, Hamp, a Philadelphia native, treasured the Leidy Medal above all.

Hamp's impact on science was not limited just to his remarkable research or to his list of publications that spanned six decades. He was also an excellent mentor to undergraduate, graduate, and postgraduate students, as well as an interactive colleague, collaborator, and facilitator for the research of others. This last role became particularly important after Hamp moved to Hawaii in 1971. Hamp described Hawaii as "God's gift to the evolutionist" because of its amazing endemic diversity. He and his wife, Meredith, often took visiting scientists under their wings and arranged and facilitated their research on the islands. Hamp and Meredith continued this tradition of generosity after their deaths by donating their second home on the Island of Hawaii as a research station in the fern forest area of Kilauea.

EARLY INFLUENCES AND EDUCATION

Hamp Carson was born in Philadelphia, Pennsylvania, on November 5, 1914. He came from an old Philadelphia family, where both his father and grandfather were prominent lawyers. His great-grandfather was a botanist and professor at the University of Pennsylvania. Hamp inherited his great-grandfather's microscope as a child, and was fascinated by the hidden world this antique microscope revealed. When a freshman at the University of Pennsylvania, Hamp became an avid birder. Despite this keen interest in natural history, Hamp initially majored in English with the intention of becoming a lawyer. He had no exposure to formal science until his junior year, when he took the introductory zoology course taught by Robert M. Stabler, a dynamic and innovative teacher who was also a falconer. Stabler's influence was pivotal to Hamp, who now realized that his passion was for zoology and that a career in science was possible. He changed his major to zoology and enrolled in the invertebrate zoology course at the Marine Biological Laboratory at Woods Hole in 1936 in order to have enough zoology credits to graduate. In that summer course he met his future wife, Meredith Shelton. A chance encounter with Calvin and Philip Bridges in the laboratory mess hall directed his biological interest toward genetics.

After graduating in zoology in 1936, Hamp remained at the University of Pennsylvania to pursue his Ph.D. (1936-1943). After several false starts, Hamp did his dissertation under the supervision of Professor Charles W. Metz, who had been a student of Thomas Hunt Morgan. While Hamp was a graduate student, the great evolutionary geneticist Theodosius Dobzhansky visited the laboratory, a visit Hamp recalled as "marvelous!" Hamp had read Dobzhansky's classic book *Genetics and the Origin of Species,* and what interested him most was that Dobzhansky showed how you could synthesize genetics with evolutionary studies on natural populations through cytology. This synthetic approach became a hallmark of much of Hamp's work.

Hamp's doctoral work was largely cytogenetic in nature and dealt with the characterization and geographical distribution of variability in the polytene chromosomes of the fly *Sciara.* He also was able to show cytologically how inversion heterozygosity can suppress crossing-over in the chromosomal region spanned by the inversion (1946). This meant that blocks of genes could be preserved as evolutionary units. This observation would influence much of Hamp's later work, with his ideas about recombination and coadapted blocks of genes playing an important role in adaptive evolution.

When Hamp was completing his dissertation work in November 1942, Viktor Hamburger, then the chair of the Zoology Department at Washington University in St. Louis, offered Hamp a position as an assistant professor. Hamp decided to accept this offer. His Philadelphian relatives were not enthusiastic about this decision, regarding St. Louis as a frontier town far from the civilized world of the East Coast. Hamp drove to St. Louis in January 1943. Meredith and their young son, Joseph, followed by train shortly thereafter.

THE WASHINGTON UNIVERSITY YEARS (1943-1971)

Hamp thrived in the stimulating and congenial intellectual atmosphere that he found at Washington University. He was particularly impressed by the intellectual guidance and warm personality of Viktor Hamburger. Another recent arrival in the Zoology Department was Harrison ("Harry") D. Stalker, who had completed his Ph.D. on *Drosophila* in Curt Stern's laboratory at Rochester, New York. Hamp and Harry developed a collaborative research program on the genetics of natural populations, mostly of *Drosophila*, with special reference to chromosomal polymorphisms and their maintenance. One of their most important projects dealt with *Drosophila robusta* and resulted in a series of classic papers published during 1945-1956. The idea of working on *Drosophila robusta*, a species found in the hardwood forests in the eastern half of the United States, arose from a letter Harry had written to the great geneticist Alfred H. Sturtevant at the California Institute of Technology. In response to some questions Harry had posed in that letter, Sturtevant suggested that he work on *D. robusta* because it had numerous inversions that were associated with size, growth rates, and other morphometric characteristics. Sturtevant also generously sent Harry and Hamp a manuscript outlining his initial observations on *D. robusta*, telling the young pair of investigators that they could do with his findings whatever they wanted, as he was not going to publish it. Thus began a highly productive collaboration, with Harry initially concentrating on the morphometrics, Hamp on the cytogenetics, and both on the ecology. They showed that specific inversions were adaptive to particular sets of environmental conditions (seasonal, climatic, and microclimatic) and provided one of the best examples of how an organism can adapt to temporally and spatially heterogeneous environments. They also made fundamental discoveries about the ecology of many species of *Drosophila*, including the fact that the larval food substrate of *D. robusta* was sap exudations of the American elm. This ecological knowledge allowed them to place their cytogenetic and morphometric surveys into the context of the ecological niche of this species. By integrating their ecological studies with cytogenetic surveys, this work quickly became a classic in the field of ecological genetics.

Another important observation that emerged from their *D. robusta* work was the distinction between populations in the center versus the margins of a species' range. Marginal populations were found to be much more homozygous for inversions, which in turn meant that their genomes were subject to far more recombination and could potentially harbor much variation (a prediction confirmed in 1973 by one of Hamp's graduate students, Satya Prakash, with the use of protein electrophoresis). The geographically marginal populations were often marginal in an ecological sense as well. This combination of less chromosomal polymorphism, greater potential for recombination, much genetic variability, and stressful ecological conditions meant that marginal populations were potentially more likely to experience novel evolutionary trajectories than the central populations. This central-marginal distinction would prove important to Hamp's thinking about speciation in his later work on the Hawaiian *Drosophila* project. Hamp's idea that marginal populations could harbor much genetic variation clearly differentiated his thinking from that of Ernst Mayr (1954) at Harvard. Mayr also speculated about marginal populations being important in speciation but had conceived of them as lacking genetic variation.

Nearly 50 years after Harry and Hamp initiated their work on *D. robusta,* Max Levitan, who had worked with them on part of the initial project, conceived the idea of resampling the populations to see how *D. robusta* had evolved in response to the climatic changes that had occurred in the last half century as well as microclimatic changes caused by localized human development. Although Hamp did not personally participate in this resampling, he enthusiastically embraced the idea and helped Max recruit others to resample these old sites. The results showed that *D. robusta* had indeed evolved considerably in response to climatic and microclimatic changes over the past 50 years; moreover, the direction of these changes was well predicted by the inferences made by Hamp and Harry some 50 years before (Levitan and Etges, 2005).

As the years went by, Hamp and Harry each developed their own research directions, although they still collaborated to some extent and always remained close friends. Even when they did not publish together, there was much synergism between the two. For example, Harry discovered that some species of *Drosophila* were capable of facultative parthenogenetic reproduction even though they normally reproduce sexually. Hamp was intrigued by the existence of parthenogenesis in *Drosophila,* and he quickly discovered other species that were capable of facultative parthenogenesis, including *D. robusta.* Hamp used artificial selection for parthenogenesis on one such species, *D. mercatorum,* to create strains capable of both sexual reproduction and efficient parthenogenesis. The resulting sexual and parthenogenetic strains were extremely powerful tools for investigating the quantitative genetic basis of fitness and other complex traits. Hamp also discovered an all-female species, *D. mangabeirai,* that reproduced exclusively by parthenogenesis in nature.

His cytological investigations revealed that *D. mangabeirai* is diploid and has normal meiosis, with diploidy being restored by the fusion of two pronuclei that had separated at meiosis I. *D. mangabeirai* also had chromosome inversions that suppressed recombination in almost the entire genome. These inversions, coupled with fusion of the products of meiosis I, induced a genetic state of permanent heterozygosity for most of the genome. Hamp generalized this observation and realized that many plant and animal species also have systems of reproduction that result in permanent heterozygosity, although the mechanisms differ greatly from species to species. He then developed a theory for the conditions under which such permanent heterozygosity would be favored and evolve (1967).

THE HAWAIIAN DROSOPHILA PROJECT

In 1962 Hamp attended a meeting in Texas. Wilson Stone, from the University of Texas at Austin, asked Hamp and Harry to join him the following summer on a project that Stone and Elmo Hardy from the University of Hawaii were organizing. The goal of this project was to study the native *Drosophila* in the Hawaiian archipelago. Hamp and Harry agreed, and soon they were an integral part of the Hawaiian *Drosophila* project. Hamp became the central figure and leader of this project after the death of Stone in 1968. From that point on, the Hawaiian *Drosophila* project was the central, but not exclusive, focus of Hamp's work for the remainder of his scientific career. Hamp moved to Hawaii in 1971 as a professor in genetics at the University of Hawaii, Manoa. Even after Hamp's retirement in 1985, he remained in Hawaii and continued to work enthusiastically on this project until shortly before his death from bladder cancer in 2004.

When this project began, it was believed that there might be 300 species of *Drosophila* endemic to the Hawaiian Islands.

A series of landmark papers by Hamp and his associates revealed that about 1000 species evolved on these islands, representing about a quarter of all the Drosophilids in the entire world. Moreover, these endemic Hawaiian species include many of the most morphological, behavioral, and ecological extremes in the genus *Drosophila*. The endemic Hawaiian *Drosophila* provide one of the most spectacular examples of adaptive radiation on this planet.

Hamp and Harry initially focused upon constructing a detailed phylogeny of these species, using cytogenetic markers (later confirmed and refined with molecular data). By overlaying their estimated phylogenetic tree upon the detailed geological knowledge of the ages of the various Hawaiian islands, Hamp was able to show that most of this amazing diversity arose from immigration from older to younger islands, with the newer species tending to live in habitats similar to those occupied by their ancestral species but nevertheless showing extreme divergence in morphology and sexual behavior. Because the major islands are separated by deep ocean barriers with no land connections, either present or past, and are oriented perpendicular to the prevailing winds, Hamp speculated that most of these interisland immigration events were extremely rare and involved only a few individuals, indeed, most likely a single gravid female. Further, because the new population tended to occupy the same type of habitat as the ancestral species, Hamp speculated that the successful founder events would be followed by a rapid increase in population size as the flies exploited this unoccupied habitat on a new island. Hamp amassed considerable evidence for these hypotheses, and they were subsequently confirmed by molecular data that are sensitive to these demographic scenarios.

THE FOUNDER-FLUSH SPECIATION MODEL

When the Hawaiian Drosophila project began, the standard model for animal speciation was the allopatric model in which an ancestral population is split into two or more subpopulations by a geographical barrier that prevents genetic exchange. The isolated subpopulations were then regarded as undergoing a gradual genetic divergence as they adapted to the different environments found in their respective geographical areas. Genetic isolation (speciation) would arise gradually as an indirect consequence of this adaptive divergence. The biogeographical pattern that Hamp observed in the Hawaiian *Drosophila* satisfied the first part of this model: a founder event on a new island would establish a geographically isolated subpopulation relative to the ancestral species. However, the observation that the new species on the younger island generally occupied the same ancestral habitat would minimize the selective pressure for adaptive divergence. Unexpectedly, the new Hawaiian *Drosophila* species typically showed extensive morphological and behavioral divergence from the ancestral species even without ecological divergence. The divergence in morphology and behavior often led to strong premating isolation. Moreover, because of the known geological ages for the Hawaiian volcanoes, Hamp could infer that this extensive morphological and behavioral divergence evolved extremely rapidly and not gradually. Hence, the slow, gradual adaptive divergence of populations did not fit the pattern observed in the Hawaiian *Drosophila*. Hamp realized that some other mechanism besides gradual adaptive divergence was needed to explain the observed speciation patterns.

To solve this dilemma Hamp returned to an idea he first put forward in 1955. Ernst Mayr, one of the central figures in the 20th-century evolutionary synthesis, had put forward a model of speciation known as “genetic revolution” in 1954.

In Mayr's model, isolated populations were founded on the periphery of an ancestral species' range, and the strong genetic drift that these founder populations underwent would cause them to lose most of their genetic variation. Because evolution is a historical process, the trajectory of a population's evolution is strongly dependent upon its starting conditions, and these initial conditions would have been strongly altered by the founder effect in Mayr's model. These altered initial conditions in particular would change the fitness effects of all remaining polymorphisms and of all subsequent mutations. Although genetic revolution is often incorrectly portrayed as a model of speciation caused by random genetic drift, in reality, genetic revolution in Mayr's model is driven by natural selection, with the selective trajectory having been changed by the strong interaction between drift and selection. The idea of a strong interaction between drift and selection that could alter selectively driven evolutionary trajectories appealed to Hamp, but he disagreed with Mayr that these peripheral founder populations would experience a substantial loss of genetic variation. Indeed, his work on *D. robusta* indicated that the peripheral populations should experience more recombination because they were less likely to have inversion polymorphisms. As a consequence, the peripheral populations had greater potential for recombinational variation than the central populations. Therefore, in direct opposition to Mayr's idea, Hamp felt that the marginal populations could be more responsive to selection immediately after the founder event, and that their rate of evolution would not depend upon the slow accumulation of newly arising mutations. Hamp empirically tested this idea of enhanced responsiveness to selection in peripheral populations in 1958 and found that the marginal populations of *D. robusta* were indeed more responsive to artificial selection than the central ones.

Hamp discovered a similar pattern for inversion polymorphism in the Hawaiian *Drosophila*. Very few inversion polymorphisms survived the founder events, so that the new founder populations would experience higher rates of recombination. Furthermore, these founder populations would be placed into an open ecological niche, and hence undergo rapid population growth, or a population "flush." Standard population genetic theory indicated that even a small founder population would lose little of its genetic variation if the founder event were soon followed by a flush. Moreover, standard population genetic theory indicated that new mutants, both neutral and beneficial, have greatly increased survival probabilities in a growing population. As in Mayr's model, the founder populations would experience large changes in allele frequencies due to the founder event, which in turn would alter selective trajectories for the surviving polymorphisms and subsequent mutations. The newly established founder population would be extremely responsive to natural selection and could experience rapid, selectively driven change because the founder-flush population would not lose much genetic variation overall, because new mutants would have increased chances for survival, and because there would be more potential recombination. This founder-flush model of speciation was first published in 1968 although Hamp refined it afterward to incorporate new discoveries.

The founder-flush model was strongly criticized by some, but mostly on the basis of mistakenly equating it to Mayr's genetic revolution model or presenting it as a model of random speciation caused by genetic drift. In reality the founder-flush model treats genetic drift as a trigger to alter selectively driven evolutionary trajectories. Hamp emphasized that his model, because it makes specific predictions about the conditions under which a founder event facilitates speciation and when it does not, was an empirically testable model of speciation, as shown by his earlier experiments on *D. robusta.* Indeed, there have been many experimental tests of this model, and a meta analysis of both the successes and failures of founder events to induce the evolution of reproductive isolation indicates that the predictions of the founder-flush model are strongly confirmed. Hamp never intended the founder-flush model to be a universal model for speciation, but rather a specialized model that is applicable in some but not all circumstances. However, when the conditions are right for founder-flush speciation, the results are spectacular adaptive radiations, such as that illustrated by the Hawaiian *Drosophila.*

HAMPTON CARSON'S LEGACY

Hamp was above all a synthesizer who brought together in his work the disciplines of genetics, cytology, ecology, and evolutionary biology. He combined field and laboratory work to understand the evolution of populations in nature. Hamp published nearly 300 scientific papers. He also wrote a book, *Heredity and Human Life,* which stressed the importance of genetics in interpreting human life. Hamp maintained a long-term interest in human genetics, motivated in part by his second son, Edward ("Eddy"), being born mentally impaired because of Rh incompatibility. Hamp and Meredith enriched Eddy's life to bring him to his full potential, and Eddy came to love nature with the same passion shown by his parents. Eddy eventually had to be institutionalized, but Hamp and Meredith would bring him on extended trips to Hawaii, where Eddy particularly loved staying at their rainforest cabin near Kilauea on the Island of Hawaii.

Besides the Leidy Medal that he was awarded in 1985, Hamp received many honors throughout his long career. He was a member of Phi Beta Kappa and Sigma Xi, and at various times served as president of the Society for the

Study of Evolution (founding member), Genetics Society of America, and American Society of Naturalists. In 1978 he was elected to the National Academy of Sciences and the American Academy of Arts and Sciences.

Hamp's interest in natural populations coupled with his passion for natural history also led him to be a strong advocate for conservation, particularly in Hawaii with its great biodiversity and equally great threats to that diversity. The conservation initiatives that Hamp promoted have helped to protect many areas and species in Hawaii.

Hamp was brilliant yet modest and always went out of his way to help and nurture others. The Hawaiian *Drosophila* project alone served as a training ground for more than 400 undergraduate, graduate, and postgraduate students in all aspects of evolutionary biology. He both challenged and motivated the minds of his students and colleagues. He infected all who knew him with his love for the natural world and our need to understand it. He stimulated a love for nature in his students not only through his science but also through his art. Hamp became a master at bonsai culture, and one of the few areas in which his personal pride of accomplishment was visible was when he was displaying his bonsai collection to his students, colleagues, and friends. Meredith was Hamp's partner in showing the beauty of nature through art, but in her case through her volumes of published poetry, much of which was inspired by her field experiences with Hamp.

In May of 2004 just months before his death, Hamp made his last visit to Washington University to deliver a seminar on his still ongoing research and to visit his son, Eddy, who lived in an institution near St. Louis. Hamp flew overnight from Hawaii, arriving in St. Louis in the early morning. He refused an opportunity to rest after this tiring journey, and instead wanted to go directly to the field sites that were being resampled for *D. robusta* as part of Max Levitan's revival of the *D. robusta* project. Hamp was excited to see these sites once again, and he was constantly observing new details and the changes that had occurred in the intervening 50 years. The little boy who was in awe of the biological world revealed by his great-grandfather's microscope was still very much present in this 90-year-old man who had never lost his passion and curiosity about the natural world.

REFERENCES

Allen, G. E. 2008. Carson, Hampton Lawrence. In *New Dictionary of Scientific Biography,* pp. 59-64. Farmington Hills, Mich.: Gale Group.

Anderson, W. W., K. Y. Kaneshiro, and L. V. Giddings. 1989. Hampton Lawrence Carson: Interviews toward an intellectual history. List of publications from 1934 to 1989. In *Genetics, Speciation, and the Founder Principle,* eds. L. V. Giddings, K. Y. Kaneshiro, and W. W. Anderson, pp. 3-41. Oxford: Oxford University Press.

Kaneshiro, K. Y. 2005. Hampton L. Carson (1914-2004). *J. Hered.* 96:285-286.

Levitan, M., and W. J. Etges. 2005. Climate change and recent genetic flux in populations of *Drosophila robusta. BMC Evol. Biol.* 5:4.

Mayr, E. 1954. Change of genetic environment and evolution. In *Evolution as a Process,* eds. J. Huxley, A. C. Hardy, and E. B. Ford, pp, 157-180. Princeton, N.J.: Princeton University Press.

Prakash, S. 1973. Patterns of gene variation in central and marginal populations of *Drosophila robusta. Genetics* 75:347-369.

SELECTED BIBLIOGRAPHY

1946

The selective elimination of inversion dicentric chromatids during meiosis in the eggs of *Sciara impatiens. Genetics* 31:95-113.

1947

With H. D. Stalker. Gene arrangements in natural populations of *Drosophila robusta* Sturtevant. *Evolution* 1:113-133.

1951

With H. D. Stalker. Natural breeding sites for some wild species of Drosophila in the eastern United States. *Ecology* 32:317-330.

1955

The genetic characteristics of marginal populations of *Drosophila. Cold Spring Harbor Symp. Quant. Biol.* 20:276-287.

1958

The population genetics of *Drosophila robusta. Adv. Genet.* 9:1-40.

1959

With W. H. Murdy. Parthenogenesis in *Drosophila mangabeirai. Am. Nat.* 93:355-363.

1961

Heterosis and fitness in experimental populations of *Drosophila melanogaster. Evolution* 15:496-509.

1963

Heredity and Human Life. New York: Columbia University Press.

1967

Selection for parthenogenesis in *Drosophila mercatorum. Genetics* 55:157-171.

Permanent heterozygosity. In *Evolutionary Biology*, vol. 1, eds. Th. Dobzhansky, M. K. Hecht, and W. C. Steere, pp. 143-168. New York: Appleton-Century-Crofts.

1970

With D. E. Hardy, H. T. Speith, and W. S. Stone. The evolutionary biology of the Hawaiian Drosophilidae. In *Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky,* eds. M. K. Hecht and W. C. Steere, pp. 437-543. New York: Appleton-Century-Crofts.

Chromosome tracers of the origin of species. *Science* 168:1414-1418.

1974

Three flies and three islands: Parallel evolution in Drosophila. *Proc. Natl. Acad. Sci. U. S. A.* 71:3517-3521.

1975

Genetics of speciation at the diploid level. *Am. Nat.* 109:83-92.

1976

With K. Y. Kaneshiro. *Drosophila* of Hawaii: Systematics and ecological genetics. *Annu. Rev. Ecol. Syst.* 7:311-345.

Inference of the time of origin of some *Drosophila* species. *Nature* 259:395-396.

1979

With P. J. Bryant. Change in a secondary sexual character as evidence of incipient speciation in *Drosophila silvestris. Proc. Natl. Acad. Sci. U. S. A.* 76:1929-1932.

1983

Chromosomal sequences and interisland colonizations in Hawaiian *Drosophila.* G*enetics* 103:465-482.

1984

With A. R. Templeton. Genetic revolutions in relation to speciation phenomena: The founding of new populations. *Ann. Rev. Ecol. Syst.* 15:97-131.

1987

The genetic system, the deme, and the origin of species. *Annu. Rev. Genet.* 21:405-423.

1990

Increased genetic variance following a population bottleneck. *Trends Ecol. Evol.* 5:228-230.

1993

Human genetic diversity, a critical resource for man's future. *Biol. Philos.* 8:33-45.

1997

Sexual selection: A driver of genetic change in Hawaiian Drosophila. J. *Hered.* 88:343-352.

2002

Female choice in *Drosophila*: Evidence from Hawaii and implications for evolutionary biology. *Genetica* 116:383-393.

2003

Mate choice theory and the mode of selection in sexual populations. *Proc. Natl. Acad. Sci. U. S. A.* 100:6584-6587.