

Always an eccentric?: a brief biography of Motoo Kimura

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Despite Motoo Kimura's enormous international reputation as a population geneticist, his work is far less esteemed in his homeland of Japan than elsewhere in the world. The most common explanation for Kimura's lack of recognition in Japan is that Kimura was too eccentric a personality to be accepted by Japanese society. This article focuses on the life of Motoo Kimura, especially on his interactions with Japanese society. Since I was privileged in having had the opportunity to personally associate with this esteemed researcher, in this article I also share some personal anecdotes of my experiences with him and my subjective views of his personality formed during my association with him at Japan's National Institute of Genetics.

Some insights into the personality of Motoo Kimura

In September 1992 I began research on the history of the nearly neutral theory at the National Institute of Genetics (NIG) in Japan, the research institute that was home to Kimura, the advocate of the neutral theory, and Tomoko Ohta, the advocate of the original and advanced models of the nearly neutral theory and his long-time associate. In early summer of the following year, towards the end of my stay, Kimura fell ill. That November he was diagnosed as suffering from amyotrophic lateral sclerosis (ALS). Although observing the progression of his illness was deeply troubling to Kimura's friends and colleagues, we would hardly have anticipated his accidental death one year later.

On 13 November 1994, his seventieth birthday, Motoo Kimura died owing to a brain haemorrhage, the result of a blow to his head following a fall in the hallway of his home. Because his arms were paralysed as a result of ALS, Kimura had been unable to break his fall. When I received news of his death from Ohta, I was stunned. Not long before, during a conversation about researchers who had studied population genetics under his guidance, Kimura had told me, 'By the way, you will probably be my last student.'¹

Three and a half years earlier, in Mishima, Japan, I had waited with my husband, Robert Steen, to meet Kimura for the first time. We had been invited to join a small group of geneticists for dinner. I was nervous. Kimura not only commanded enormous respect as an eminent figure in the field of population genetics, but his imposing stature as a scientist was coupled with his reputation (at least in the United States) as a proud and stubborn man. Kimura arrived a few minutes late, entered the restaurant's lobby with Ohta, and walked briskly towards us, extending his right hand. Greeting him in Japanese, I stepped forward to shake his hand but, ignoring me, Kimura greeted my husband in English and shook his hand instead. I was somewhat taken aback. However, as I began to learn more about Kimura, I came to realize that he had not intended disrespect towards me as a female, but rather was trying to help my husband, a literature scholar, feel less isolated among a group of geneticists.

Gradually I became aware of many of the less apparent sides of Kimura's personality, and came to recognize him as a very sweet and caring person. He often enquired about my family's health, my husband's research, and my daughter's kindergarten experiences. As my family prepared for our move to Japan, Kimura even joined Ohta in apartment-hunting for us. Especially with small children, he was very kind, and his smile for small children was unfailingly sweet. When Kimura played with his granddaughter, Hanako, the severe scientist was completely obscured by the doting grandfather. He prepared a pair of special slippers for my daughter Lisa to wear when we visited his home. In fact, he often presented me with small gifts for her, saying: 'I found some cute things downtown. Will you give these to Lisa?'

Kimura enjoyed shopping and, on the way home from work, he often stopped to shop for groceries for himself and his wife. He enjoyed telling jokes and watching Ohta and me laugh. He was relaxed with the researchers in his lab, with Ohta, and with me. As the centre of a scientific controversy, perhaps Kimura had few opportunities to show the softer side of his personality to scientists who did not know him well.

By all accounts, Kimura was an excellent teacher who respected the originality of each researcher in his charge. Although he never had the official opportunity to take on students, many researchers still regarded him as their teacher. Reciprocally, Kimura regarded these researchers as his students and told me that he cared about them. Among those who thought of Kimura as a life-long teacher is Naoyuki Takahata, the renowned specialist in MHC (major histocompatibility complex)². As a young researcher, the eminent molecular evolutionist Masatoshi Nei also visited Kimura regularly to learn about population genetics³. And, of course, although Kimura sometimes disagreed with Ohta with regard to matters of science, he nevertheless allowed her to pursue her research freely at NIG and took an active role in promoting her career⁴.

When a British journalist asked Kimura what he thought about the common perception that the Japanese lack originality, Kimura answered: 'The Japanese educational system emphasizes that students follow others, and this tendency terminates students' originality and outstanding talents. I feel sorry for the young people.'⁵ Kimura had been regarded as an eccentric individual from childhood, and his personal difficulties as a child in the Japanese educational system no doubt motivated him to promote talented young scientists without the restrictions he had endured.

The life of a pioneer scientist⁶

Motoo Kimura was born on 13 November 1924 in the castle town of Okazaki, near Nagoya. One of Kimura's ancestors was a traditional casting artisan well known for making large temple bells (*dai bonsho*). About his parents Kimura said: 'My parents were just like the ones in Thomas Mann's novel *Tonio Kroger*. My father was thoughtful but stubborn, and my mother was artful and optimistic.'⁷

Like his mother, Kimura was optimistic and outspoken. One Japanese journalist has argued that these personality traits may have helped Kimura present the 'eccentric' neutral theory of molecular evolution to the world without hesitation⁸. However, although Kimura's bright outlook and capacity to speak his mind were clearly beneficial, he disliked controversy⁹. At the time that he published his first paper on the neutral theory, Kimura said he did not realize the strength of the impact it would have internationally on evolutionary biology; he was simply unaware that challenging selectionism in the Western scientific communities would be problematic¹⁰.

Kimura's capacity for flexibility and inventiveness certainly contributed to his development of the neutral theory. When Kimura obtained his first data for the neutral theory, he was unsure of how to interpret them. His education in the US had predisposed him to believe that the selection theory was a universal evolutionary theory. Only later did he realize that his data could only be supported by a different argument. As he gathered more data with the help of Ohta, Kimura became increasingly convinced by his findings.

Like his father, Kimura was very focussed. As a child, however, this personality trait sometimes worked against him. His parents often scolded him for concentrating on one task to the exclusion of other important tasks. Kimura's boyhood pastimes were fishing, Japanese chess (*shogi*), chemistry experiments and, especially, horticulture and botany, which he first encountered at the age of three or four while watching his father taking care of plants at his garden. When he was small, Kimura remembered, he thought a machine-like object existed inside each seed and bulb to create the stems and flowers.

Kimura attended elementary school in wartime Japan, and was unable to conform to the uniformity of the patriotic educational system, where students were expected not to ask too many questions. Kimura often irritated his teachers with more questions than they could answer and, for this reason, was regarded as a 'bad' student. Soon he lost interest in his studies. 'I hated going to school,' he laughed, 'so I almost flunked. I just could not wait to graduate from school and be done with that painful experience.'¹¹ However, in fifth grade, Kimura met an exceptionally open-minded and dedicated teacher, one of the very few teachers, Kimura felt, who went out of their way to help students as much as possible.

This teacher changed the course of Kimura's life. Under his tutelage and encouragement, Kimura's interest in his studies was rekindled and, in 1937, Kimura decided to continue his education at Okazaki Middle School, where he again encountered a dedicated science teacher. Kimura's goal was a career in botany and, every weekend, he travelled the seven or so miles from his home to Kuwagai Mountain to collect plants, which he later examined with his teacher. Kimura was so serious about these projects that his fellow students jokingly called him 'Professor Botany'.

Kimura's third year of middle school in 1939 was pivotal. His family was stricken with food poisoning, and his youngest brother, only eight years old, died as a result. This was the saddest experience of Kimura's childhood. Confined to bed as a result of his illness, Kimura continued his studies in the hope of catching up with his schoolwork, and it was during this time that his interest in mathematics was kindled. He so much enjoyed geometry and was so successful in his study of mathematics that his math teacher, Mr Kuroda, suggested that he become a mathematician. Young Kimura felt torn between his interests in botany and mathematics; he could give up neither. He was, of course, as yet unaware that his two fields of interest could be merged into a single pursuit.

In 1942 Kimura went on to attend Eighth High School (*Daihachi kôtô gakko*), now Nagoya University, where he met the outstanding plant morphologist Dr Masao Kumazawa. Under Kumazawa's guidance, Kimura conducted morphological studies of lily chromosomes and made his academic debut through the publication of four outstanding papers that he wrote with Kumazawa. Through Kumazawa's lectures, Kimura learned about Dr Hitoshi Kihara, a pioneer cytogeneticist well known for his work on the wheat genome; Kimura dreamed of working with Kihara.

In 1944, when Kimura advanced to Kyoto University, where Kihara was a member of the Faculty of Agricultural Sciences, the fulfilment of his dream seemed possible.

However, Kihara advised Kimura to enter the Faculty of Science, where he would be granted exemption from compulsory military service by the Japanese government. Following Kihara's counsel not to waste his education by going to war, Kimura majored in cytology at Kyoto University's Department of Botany in the Faculty of Science. However, his relationship with his advisor at his laboratory was poor; the two often quarrelled.

Kimura could not give up his interest in genetics; he took almost all the genetics courses offered at Kyoto University. He also read major papers in the field to teach himself various theories of genetics. When he encountered a pirated version of Dobzhansky's famous work, *Genetics and Origin of Species*¹², Kimura began to consider the connections between mathematics and genetics. Could he, he wondered, develop a field of theoretical genetics? Kimura recalled: 'Most of my fellow students did not understand why I, a cytology student, was interested in mathematics. They even told me I was wasting my time in a useless pursuit.'¹³ Kimura often visited his cousin and her husband, Dr Matsuhei Tamura, in Kyoto. Tamura was then an assistant professor of theoretical physics working under the Nobel laureate Dr Hideki Yukawa at Kyoto University¹⁴. Over dinner, Tamura and Kimura often discussed theoretical physics.

When Kimura graduated in 1947 the Pacific War was over and compulsory military service had been abolished. Kimura returned to his dream of working with Hitoshi Kihara. In addition to holding his professorship at Kyoto University, Kihara also headed a research institute, Kihara Biochemical Institute, in Kyoto¹⁵. Kimura entered the Kihara Institute as a research associate. There he finally encountered the field of population genetics, a field that had not yet been introduced to Japan, through his reading of Sewall Wright's 1931 paper, 'Evolution in Mendelian populations'.¹⁶ Kimura so admired this paper that he often took the four-hour train trip to the Tokyo University library to research Wright's other papers, hand-transcribing them into his notebooks so that he could study them later.

Kimura worked at the Kihara Institute for two years and then, under Kihara's recommendation, entered the newly established National Institute of Genetics (NIG). He often reminisced nostalgically about the early days of the NIG, which was originally housed in a two-storey wooden structure that had been the wartime Nakajima Airplane Factory (*Nakajima Hikouki*). In the early post-War era, NIG, which was insufficiently supplied with research materials and literature, did not provide a hospitable environment for researchers; some researchers left owing to its poor facilities. To compensate for NIG's limited supply of research literature, Kimura continued his visits to the Tokyo University library to read foreign journals.

At that time Kimura was the only person in Japan pursuing the mathematical study of genetics, and his work was often severely criticized by his colleagues at NIG and the Genetics Society of Japan. In November of 1951 he presented a lecture based on his mathematical model of genetics, 'Evolution of substable population', at the Genetic Symposium at Sakata Farm. One reviewer wrote:

No living thing appeared in Kimura's morning talk, . . . Throughout his talk, what we saw was only the acrobat of numbers. Even those distinguished scientists who could comprehend 'sleep talking' of flies were stunned by Kimura's talk. It is certainly questionable if there is any future prospect in this kind of study or not.¹⁷

However, an opportunity for Kimura to cultivate his talent in the US soon arrived. A geneticist with the Atomic Bomb Casualty Commission (ABCC), Duncan

McDonald, who was visiting Hiroshima to study the genetic effects of the atomic bomb, heard about Kimura and met with him¹⁸. McDonald was so impressed by the superb understanding of population genetics Kimura had attained without any official training in the field that he immediately arranged for Kimura to study in the US. Between 1953 and 1956, Kimura studied population genetics at Iowa State College (Ames) and the University of Wisconsin (Madison), and he associated with outstanding population geneticists including Sewall Wright and James Crow¹⁹.

When Kimura received his Ph. D. from the University of Wisconsin in 1956, he also sent his dissertation to Kyoto University and applied for a Ph. D. This application was rejected because Kimura's committee at Kyoto University regarded his dissertation as too mathematical in nature to be honoured by a biology department. Although Kimura later was awarded a Ph. D. by Osaka University, in general he continued to experience difficulty in getting his work understood by Japanese biologists.

In the early 1960s three molecular biologists, Emile Zuckerkandl, Linus Pauling and E. Margoliash, used comparative studies on amino-acid sequences of haemoglobin and cytochrome *c* among vertebrates and found that the rates of amino-acid substitution in these proteins were approximately the same in various mammalian lineages. In 1965 Zuckerkandl and Pauling proposed the molecular clock hypothesis²⁰. Two years later, Kimura used their molecular clock hypothesis to calculate the evolutionary rate of the entire genome of several animals. This molecular clock hypothesis became a useful tool that enabled population geneticists and molecular biologists to estimate the rates of amino-acid substitutions.

In the late 1950s and the early 1960s Kimura was interested in the concepts 'genetic load' discussed by H.J. Muller and 'cost of natural selection' proposed by J.B.S. Haldane²¹. By studying Haldane's 'cost of natural selection' argument, Kimura noticed that Haldane's model disregarded the effect of the random sampling of gametes in a finite population. Therefore Kimura recalculated the cost of substitutional load in a finite population by using a diffusion equation, and noticed that evolutionary change far exceeded the maximum rate under natural selection as predicted by Haldane.

To explain this discrepancy, Kimura developed what was to become his lifework, the neutral theory of molecular evolution²². He argued that the great majority of evolutionary changes at the molecular level are not caused by Darwinian selection, but by the random drift of selectively neutral or nearly neutral mutants. Ohta, who was then Kimura's research associate, helped him calculate additional data to back up his original data set.

Kimura presented his theory at a domestic meeting of the Genetic Society in Fukuoka in the autumn of 1967, but his paper received very little response. The following February he published his work in *Nature*²³. The team of Jack L. King and Thomas H. Jukes had independently reached the same conclusion as Kimura and, in the following year, they published their findings in *Science* under the provocative title 'Non-Darwinian evolution'²⁴. These publications created the enormous neutralist–selectionist (or selectionist–neutralist) controversy, and Kimura spent the rest of his life defending his theory.

In 1988, at the International Meeting of Genetics Society in Toronto, Kimura impressed the audience with his advocacy of the basis of his neutral theory, which he termed 'survival of the luckiest', as opposed to Herbert Spencer's term 'survival of the fittest'. Kimura's comments about Ohta not only shed light on this remarkable team, but also reflect his outlook on life and, perhaps, on the 'survival of the luckiest', for Kimura described his collaboration with Ohta in similar terms:

I am very lucky to have Dr. Ohta as my colleague. I know that Dr. Ohta is extremely bright—much brighter than I. The reason [that] I became a bit more famous than her is simply luck. Right now, like many of the famous scientists, I am just luckier than her. And I think [that] that may change in the future.²⁵

During his life Kimura received numerous awards and honorary memberships in professional societies, including the Genetic Society of Japan prize (1959), the Weldon Oxford University's Memorial prize (1965), the Japan Society of Human Genetics prize (1970), a US National Academy of Sciences foreign membership (1973), and the Emperor's medal (1976). Other awards included the Chevalier de l'Ordre National du Mérite (1986), the Asahi Shinbun prize (1987), the United States Academy of Science John J. Carty Award (1987), and honorary membership of the Genetic Society of Great Britain (1987). Kimura was also awarded the International Prize for Biology (1988), the British Royal Society's Darwin medal (1992), and a foreign membership of the Royal Society (1993). He was a Nobel prize nominee annually until 1994.

Of these many honours, Kimura seemed especially pleased to have received the Darwin medal, which was awarded to him by the Royal Society of London—the home of the neo-Darwinist school. This award signalled to Kimura the end of the neutralist–selectionist controversy. (Kimura was, incidentally, the first Asian biologist to be awarded the Darwin medal.) Since I was working at NIG when Kimura received this award, I was able to witness his delight; and I have a photograph of the ceremony, given to me by him, which captured the broad smile of John Maynard Smith, a powerful neo-Darwinist and severe critic of the neutral theory, as he presented the Darwin medal to Kimura²⁶.

Notes

- 1 Motoo Kimura, interview on 28 July 1993. Translated by the author.
- 2 Naoyuki Takahata, interview on 9 December 1992.
- 3 Motoo Kimura, personal conversation. Translated by the author.
- 4 Ohta developed her nearly neutral theory around 1973. Despite intense scientific disagreements between Kimura and Ohta from the late 1970s throughout the 1980s, both Ohta and Kimura reported that this disagreement never influenced their friendship and Kimura did not force Ohta to abandon her theory.
- 5 Kimura reported to this author this conversation with a British journalist. Translated by the author.
- 6 This section is based on the series of interviews with Kimura between 1 July and 28 July 1993.
- 7 Motoo Kimura, interview, 1 July 1993. Translated by the author.
- 8 Motoo Kimura, interview, 9 December 1992. Translated by the author. Kimura told me about this comment by a Japanese journalist during this interview.
- 9 When Kimura read the preprint of the paper published by King and Jukes, he suggested that the authors change the provocative title 'Non-Darwinian evolution'. Kimura told me that he did not want to provoke controversy over the neutral theory. I had also heard about this story from William Provine a year before I interviewed Kimura.
- 10 The original Darwinian theory synthesized with Mendelian genetics since the early 1900s in the US is called the 'synthetic theory'.
- 11 Motoo Kimura, interview on 3 July 1993.
- 12 The original book was written by T. Dobzhansky: *Genetics and the Origin of Species*, New York: Columbia University Press, 1941.
- 13 Motoo Kimura, interview on 28 July 1993.
- 14 Kimura later found out that Dr Tamura is actually a cousin of Ohta's mother.
- 15 This institute was later moved to Yokohama. Ohta also worked at this institute just before she came to the US for her Ph. D. work at North Carolina State University. The institute was a stepping stone for young cytogeneticists back then.

- 16 Sewall Wright, *Genetics* 16: 97–159 (1931).
- 17 *Idea* 6 (March 1952): cover page.
- 18 ABCC gathered data on the biological effects of the atomic bombs dropped on Hiroshima and Nagasaki, and hired local physicians and provided medical treatment to victims of the atomic blasts.
- 19 I shall not discuss this issue here since William B. Provine describes this period in detail in his article in this issue.
- 20 Emile Zuckerkandl and Linus Pauling, 'Evolutionary divergence and convergence in proteins' In *Evolving Genes and Proteins*, eds. V. Bryson and H. J. Vogel (New York: Academic Press, 1965), pp. 97–166.
- 21 See J. B. S. Haldane, 'The cost of natural selection' *Journal of Genetics* 55: 511–524 (1957)
- 22 Motoo Kimura, 'Evolutionary rate at the molecular level' *Nature* 217: 624–626 (1968).
- 23 Motoo Kimura, *Nature* 217: 624–626 (1968).
- 24 J. L. King and T. H. Jukes, 'Non-Darwinian evolution' *Science* 164: 788–798 (1968).
- 25 Motoo Kimura, interview on 26 July 1993. Translated by the author. Kimura's collaboration with his colleague Ohta was indeed characterized by mutual trust and respect.
- 26 This photo was taken by Kimura's younger brother, Dr Katsumi Kimura.