Of Drosophila, Butterflies and Men:
The Scientific Meaning of Extrapolation Across the Human-Animal Divide

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Introduction

Using animal and insect studies to understand the effects of nuclear exposure on humans has long been a challenge in scientific research. While this challenge is not unique across various scientific disciplines, it is particularly pronounced in fields such as toxicology, epidemiology, and radiobiology. Much of the research on the toxicity of substances and consumer product safety hinges on establishing links and extrapolations between animal and human studies. This process, driven by the need to safeguard human well-being, often begins with animal testing before proceeding to humans. Although there is a consensus within the scientific community about the importance of animal studies in identifying potential human health risks, there are also debates about the limitations of extrapolation when it comes to understanding health effects between experimental studies on animals and the complexities of human responses.

Throughout the history of scientific research, phrases such as “in animal studies” or “in human studies” have become regular precursors to discussions of substance characteristics. Nevertheless, the interpretation of the outcomes of these animal experiments is not straightforward and can vary wildly due to the nature of substances. For instance, various chemicals with toxic properties are not only carcinogenic, but could also affect brain development, heart, and kidney function, or interact differently with diverse bodies (e.g., Johnson, Wesseling and Newman 2019; Tchounwou et al. 2012; Wing 1998). This intricate web of toxic effects and their pathways, or where they might hide or accumulate to unknown effect, often extends to a combination of substances over time, a phenomenon known as “toxic layering” (Goldstein and Hall 2017).[1] While important parallels between animals and humans might, and often do, exist, the precise nature of such extrapolations remains a subject of uncertainty. The study of radiation’s biological effects on humans and animals presents an acknowledged challenge, with far-reaching consequences. The human-animal divide is perhaps best understood within a comparative and deeply historicized framework. In this essay, we critically examine the challenges of *extrapolation*, of applying findings from

[1] There is, too, an abundance of chemicals that we have not yet been able to test at all either on humans or animals. Currently there are more than 15,000 chemicals that are produced in quantities greater than 10,000 pounds per year and 2,800 are produced in quantities that exceed one million pounds annually. Reports indicate that only 43 per cent of these “high volume” chemicals have been tested for human toxicity, and only 7 percent have been evaluated for their potential effects on development. (National Scientific Council on the Developing Child 2006: 1).

animal and insect studies to the understanding of human responses to nuclear radiation. We advance two key arguments. First, we highlight the profound scientific uncertainty and complexity inherent in radiation research on two insects, resulting in the difficult and imprecise extrapolation of data from animals to humans. Second, we explore the historical and political context of nuclear research, especially during the Cold War era, where scientific uncertainty was amplified and polarized. This context, much like other research during this period, embodied the era's tensions and attitudes toward the necessity of animal research. We show that when animal studies implicate harm to humans, they are frequently dismissed based on the belief in human exceptionalism, asserting that humans are inherently different or more resilient than animals. Additionally, the selective referencing of outdated scientific research studies continues, particularly those conducted by the Atomic Bomb Casualty Commission (ABCC) and later the Radiation Effects Research Foundation (RERF) in Hiroshima and Nagasaki, Japan. This has perpetuated a form of "radiation effects denial" among humans, or at least a seeming unwillingness to consider harms taking place in the present. As a result, animal studies are often instrumentalized to bolster arguments about the safety of nuclear technologies, including nuclear power plants.

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In this essay, we focus on two distinct case studies that shed light on the complexities of translating findings from animal research to humans in their appropriate historical contexts to inquire about the animal-human line that informs our current understandings today. These case studies encompass experiments on Drosophila (fruit flies) that investigated genetic mutations and population biology in the 1940s, as well as recently concluded studies examining the biological impact of radiation and a heightened presence of mutant butterflies in Fukushima, Japan.

Theodosius Dobzhansky and Drosophila in Brazil

A 2016 doctoral dissertation in the field of social work conducted in Brazil reveals that residents living in communities within a close radius (under 10 kilometers) to the nuclear power station in Angra dos Reis, Brazil, believe that there is a frequent occurrence of genetic abnormalities in children born in the region. These residents believe these abnormalities are connected to the lack of safety of Brazil's nuclear facilities (Attianezi 2016). This perspective exists in the region, but it is not the most common perspective. It primarily appears in one thesis by a Brazilian social worker who has spent some time in these communities. At the same time, public health scholars have tried to look at cancer statistics in the region and have come up with amorphous results, including the public health team I assembled in Brazil in 2018 to examine this question. The cancer statistics that are available are

incomplete due to hospital reporting and because of the relative newness of Brazil's inclusion in globally based cancer registries. This limitation has made it challenging and frustrating to study cancer rates at a regional level. As a result, most of the scientific studies done in and around Angra dos Reis do not find statistically significant cancer spikes. This includes our own study that looked for statistically significant clustering of cancer incidence within 5 or 15 kilometers of the Angra nuclear power plants between 2007 and 2012 (McFadyen and Goldstein 2019).

While this essay is not about human genetics or even about cancer risks for populations living near nuclear power stations, it is about the historical assemblage of scientific understandings of low-dose ionizing radiation risks and how the knowledge from studying model organisms—here, Drosophila—built upon a long history of experimentation among those organisms. Our goal is to understand how the assemblage of knowledge about model organisms helped shape our reasoning and understandings of radiation risks to humans and to connect this assemblage to the most powerful study of radiation effects that comes from the selective referencing of outdated scientific research studies of the Atomic Bomb Casualty Commission and its study of human radiation effects after the atomic bombing of Hiroshima and Nagasaki (Goldstein 2012; Goldstein and Stawkowski 2015).

The Drosopholists

This story unfolds in Brazil—Goldstein's field site—where Drosophila's significance as a gateway organism allowing portions of the scientific community to apply their expertise to human genetics and Drosophila's role in early population biology. It is also the history of some of the humans and their Drosophila companions and experiments that helped establish Drosophila as a model organism. It is not by chance that many of the personnel—evolutionary and population biologists and Drosopholists, as they were called— of the 1920s, 1930s, and 1940s moved to human organisms by the 1940s. But our interest in this story is this: What might we see in the early work of Drosopholists that informs scientific knowledge around radiation biology in humans that we see later? Many of the early Drosopholists wound up on commissions and in research institutions that were responsible for helping understand the effects of radiation on the human body. And if it wasn't them, then it was their students. Our contention is that something about Drosophila might have held on and so we are looking for those effects, as elusive as they may be.

For our purposes here, the story focuses mainly on H.J. Muller and T.G. Dobzhansky, as well as the Brazilian Drosophilists who studied with Dobzhansky and carried out collaborative projects with him between 1943 and 1960 in Brazil. Dobzhansky's fourth major visit to Brazil in the early 1950s and his work in Angra dos Reis is of special interest. Muller and Dobzhansky of course are two world-renowned Drosopholists who helped establish Drosophila as a model organism and were involved in numerous scientific debates—some with each other—that

are relevant to this history. Especially important is the time Dobzhansky spent in Brazil, helping to establish Drosophila research at the University of São Paulo, to mentor and direct fellow researchers, and to test some of his theories about Drosophila population biology, genetics, and evolution in a tropical area. Many researchers in Brazil who worked with Dobzhansky eventually studied other organisms and even humans in centers of radiobiological research such as Oak Ridge National Laboratory, Tennessee and Cold Springs Laboratories, New York and became contributing experts on radiation effects on humans (Goldstein Interviews with Carlos Vilela and André Luiz Paranhos Perondini in 2012). Indeed, both Dobzhansky and Muller lived long enough to have insights into low dose ionizing radiation on humans and as we mention in the conclusion, both participated in scientific conferences and panels evaluating radiation effects.

It is fair to say that many researchers in the early twentieth century used Drosophila as a gateway to research in human genetics and that some of what they learned in the universe of Drosophila may have influenced how they understood human genetics at a time before the discovery of DNA. Numerous colleagues extending from Dobzhansky's presence in Brazil wound up in human genetics research and participated in commissions devoted to radiation risk; their Drosophila experience was already part of their expertise and their world view. The history and knowledge about Drosophila forms part of the assemblage of understanding of the risk potential caused by low dose ionizing radiation. These risks have often been underestimated, and it is Drosophila that adds to the puzzle of risk assessment.

Dobzhansky in Brazil

The prominent Ukrainian American geneticist Theodosius Dobzhansky (1900-1975), author of *Genetics and the Origin of the Species* (1937), traveled to Brazil on four extended visits between 1943 and 1960 with support from the Rockefeller Foundation. Dobzhansky's charismatic personality was still legend among the Brazilian scientists Goldstein interviewed in 2012 and 2015 at the University of São Paulo, in kinship terms the same people or the next generation down from the principal researchers who studied directly with Dobzhansky. Somewhat ironically but also perhaps mere coincidence, Dobzhansky conducted his experiments on the islands of Angra dos Reis, in the very same region that today houses Brazil's only existing nuclear power complex in operation since 1985.

The Brazilian researchers who became Dobzhansky's academic partners were establishing their scientific disciplines at the newly formed Faculty of Philosophy, Sciences and Linguistics at the University of São Paulo and Dobzhansky's presence, direction, and global reputation afforded them the kind of intellectual cultural capital they needed to expand and to formalize high quality scientific research in Brazil. Dobzhansky's main collaborator during his early visits was André Dreyfus (1897-1952), a geneticist who was a foundational member of the University

during that period. Dreyfus' death in 1952 meant that the direction on the Dobzhansky project—still supported by the Rockefeller Foundation—was taken over by Crodowaldo Pavan (1919-2009), a population biologist and geneticist. Pavan also worked on population genetics of Drosophila, on the enlarged chromosomes observed in these organisms. However, by the 1960s, he was working at Oak Ridge National Laboratory, where he studied the effects of radiation and virus infection on chromosomal morphology and cellular genetics of Rhynchosciara, another fly. Upon his return to Brazil, he worked on questions of biological control of agricultural pests. In 2012, Goldstein interviewed some of Pavan's now elderly and mostly retired former students whose generation experienced some of the benefits of the now established and prestigious University of São Paulo and who worked still in the fields established by Dobzhansky—population biology, Drosophila genetics, and human genetics.

Recent literature reflecting on Dobzhansky's research program in Brazil has been slightly more critical of the work than earlier literature. While Dobzhansky is recognized for having aided the research program to produce a great deal of publications and created the conditions for serious research (Monte Sião and Pereira Martins 2020), it has also been suggested that his overbearing personality and excessively directive style in his research collaborations was problematic (Magalhães and Vilela 2014; Lewontin, Beatty and Krimbas 2001, Vilela, 2012 interview; Paranhos Perondini 2012 interview). Colleagues who were connected to Dobzhansky during his stay in Brazil recognized—perhaps later—that he was best defined as a Darwinian evolutionist and population geneticist rather than a classical geneticist. This difference may be a critical one, as scientists interested in populations of animals are often focusing on recovery and stability of a particular population over generations, and how things evolve over the long term and into the future, and not on individual genes and their expression. So much of this research took place prior to our basic understandings of DNA, when classical genetics was still in a very infant stage. So, while important genetics questions were being posed in the context of Dobzhansky's research, his training was not centered entirely in genetics (but instead on the evolution of populations over time). Perhaps more importantly to point out, there were problems in Dobzhansky's research design and a lack of rigor in the analysis of the results (Monte Sião and Pereira Martins 2020), and his determination to prove his own theories right may have weakened his designs and his relationships among his fellow researchers.

One of the inspirational stories of Dobzhansky's intense interest in working in Brazil is expressed in his memoir, *The Roving Naturalist* (1980) where he indicates that when he flew over Angra dos Reis and saw the many small and seemingly empty islands from above, he determined that these islands would be an excellent location for his study of Drosophila. Dobzhansky saw that these small and separate islands would constitute a kind of natural population box that could be controlled experimentally while still being in nature, a common idea about the value of island isolates for scientific study more generally in this period between the wars (see also, Goldstein 2013; Goldstein

2012; Farish 2013). Ove Frydenberg (1928-1975), a Danish researcher with a background in statistics and philosophy of science, came to Brazil to participate in the project. However, he held objections about Dobzhansky's experimental design, claiming it would not test the intended hypotheses (Magalhães and Vilela 2014: 141). According to Magalhães and Vilela (2014:142):

> The project designed by Dobzhansky consisted basically of choosing a number of genetic markers, such as lethal alleles and chromosome inversions, some originated in the local population itself and others coming from natural populations of different regions, introducing each marker in one island in great amounts and observing how they behaved over time. . . Suddenly, in certain samples, markers started to appear, i.e., certain inversions which did not exist in these populations nor had they been introduced, were found at high frequencies. Dobzhansky immediately drew his conclusions: "Frydenberg and Magalhães are sabotaging the experiments so they won't succeed!"

Later, Magalhães, the author of this reflection and a young researcher on the Dobzhansky project at the time, would have to release flies that had been created in the university laboratory at Angra dos Reis, which would then help Dobzhansky justify the muddled results. The issue, it seems, and one that the researchers could only admit decades later, was that one of the markers already existed in the natural population as a genetic marker, something Dobzhansky had a difficult time admitting. As it turns out, Dobzhansky belonged to one of two schools having to do with trying to understand the genetic diversity of natural populations, one being the mutational model and the other called the heterotic model[2]—what Dobzhansky had already written a great deal about—to be clarified ahead.

Dobzhansky's Brazilian team eventually released fruit flies that were genetically marked by radiation into this seemingly isolated natural paradise long before it housed nearby what was to be Brazil's first and only nuclear power complex. The team of researchers observed mutation in fruit flies across several generations. Another element in this story is Dobzhansky's friendship with James V. Neel, a man who also began his career as a Drosophila scholar but later carried out what is universally viewed as the *gold standard* study on the genetic effects of radiation on humans. Neel conducted his large-scale human study in his capacity as Japan-based director of the Atomic Bomb Casualty Commission (ABCC) in 1947-1948 following the atomic bombing of Hiroshima and Nagasaki. Yet he also carried out research on Brazilian Amazonian Indian tribes, extending questions about mutation, genetics, and radiation effects to (allegedly) non-irradiated populations living under the forest canopy. But to understand Neel and the importance—even until today—of the ABCC research, we need to first understand Dobzhansky's position on mutations in Drosophila.

[2] Heterosis refers to the phenomenon that progeny of diverse varieties of a species or crosses between species exhibit greater biomass, speed of development, and fertility than both parents. Various models have been posited to explain heterosis, including dominance, overdominance, and pseudo-overdominance.

Dobzhansky is remembered for many scientific contributions including integrating field and laboratory studies together and utilizing predictive mathematical models such as the Hardy-Weinberg Law (Andre, Wirtz, and Das 1989: 64)—a theory that predicts that a population will remain at genetic equilibrium if five conditions are met[3]—in his work with Drosophila. Dobzhansky had early on worked in T.H. Morgan's (1866-1945) esteemed Drosophila laboratory at Columbia University known as the "fly room" and was interested in Morgan's iconic genetic experiments with *Drosophila melanogaster* that had some senior biologists of the period calling Morgan's mutant flies monsters (deJong-Lambert 2012). Dobzhansky is perhaps the first to successfully integrate field and laboratory studies together, so the Angra dos Reis islands offered a unique natural laboratory for his later work. Morgan's "fly room" helped Drosophila become a model organism, because of its small size, requiring minimum care and having only four pairs of chromosomes. Most importantly, fruit flies breed quickly (they can lay hundreds of eggs in a few days) and live for about two weeks and share 75 per cent of the genes that cause diseases in humans. These characteristics make it easy to observe mutation rates.

One of the emerging themes of Dobzhansky's work in Brazil at the time revolved around the role of "lethal genes," which are genes that can cause the death of an organism, usually due to mutations. This topic became a critical question during the 1940s, and Dobzhansky came to Brazil believing that naturally occurring lethal genes would be less harmful than those induced by radiation. I will return to this hypothesis and its implications shortly, but first I must introduce H.J. Muller (1890-1967) who had different thoughts about naturally occurring and lethal genes, all of which also came to be thought about first in the context of Drosophila laboratories.

H.J. Muller was a student of T.H. Morgan at Columbia University and later spent close to eight years in the Soviet Union, eventually becoming disillusioned with Soviet science during the Lysenko Affair and Stalin's purges. Muller, importantly, had been the first to use X-rays to produce laboratory-generated mutations in Drosophila and his work examined the effects of these laboratory produced mutations on the genetics of the population. When he came back to the United States, he served on the commission to study the genetic impact of the atomic blasts on Hiroshima and Nagasaki survivors' unborn children and became known as a scientist who consistently warned of the effects of radiation on human genetics. Muller also won the Nobel Prize in 1946 for his work on radiation-induced gene mutations, but his work and his prize has more recently become controversial because of its lack of peer review (Calabrese 2018). Muller was apparently eager to beat out other rivals and neglected to take his work

[3] The five conditions specified in the Hardy-Weinberg no mutation and no new alleles are generated by mutation nor are genes duplicated or deleted, random mating, no gene flow, very large population size, no natural selection.

to the peer review process. During his Nobel Prize acceptance speech in 1946, he stated that mutations produced by irradiated genes are no more harmful than naturally occurring mutations, yet he still maintained concern about radiation effects. This is important to the assembled timeline here as Dobzhansky and Muller were often theoretical rivals and Dobzhansky, too, was keen on understanding the effects of both naturally occurring lethal genes as well as those produced in the laboratory. Muller remained concerned with and became known for his lifetime focus on the long-term effects of radiation.

According to the geneticist James Crow (1987: 359-360), Muller, who remained a strong natural "selectionist" throughout his lifetime, nevertheless remained concerned about radiation effects. I should mention here that Crow is a crucial scientist for understanding the post-War ABCC reports. He headed a committee in 1975 to review the original report. According to Crow, Dobzhansky, somewhat differently than Muller, favored a theory of "overdominance" and highlighted the importance of "lethal genes," the same lethal genes that became controversial in the Drosophila research in Brazil. Dobzhansky believed that since the lethal genes present in natural populations were subject to natural selection, they would be less deleterious than new genes introduced by exposure to radiation. So, a point of agreement, one could say, is that both Muller and Dobzhansky were both selectionists, but differed on the extent of damage into the future that they envisioned could be produced. However, the Brazilian researchers summarizing the findings concluded their paper as follows:

> These data clearly point out that in the laboratory there is no difference between the effects of irradiated lethal genes and natural lethal genes in hybrids of *Drosophila willistoni*. The experimental data therefore did not support the hypothesis that lethal genes newly introduced by radiation could produce more drastic effects than the ones produced by natural lethal genes in heterozygosis. (Pavan et al. 1958: 207)

It seems that Dobzhansky was intent in Brazil on showing that naturally occurring genes would be less deleterious than irradiated genes, but that the data did not bear out this hypothesis and Brazilian researchers eventually confirmed this finding in their long list of publications. Some have argued that their disagreements about the differences between lethal genes produced in the laboratory and naturally occurring ones created divisions among the researchers. This excerpt is from Monte Sião and Pereira Martins' (2020: 264) paper about these expeditions:

> Among the factors that could have contributed to the decrease in joint publications of Dobzhansky and the Brazilians we can also add the divergence between them concerning some scientific subjects, such as the effect of lethal genes. Beginning with Dobzhansky's second visit (1948–1949) until the fourth one (1955–1956), this issue was under discussion. Some years later, a group of eight Brazilians published papers challenging Dobzhansky's hypothesis (see also Pavan and Brito da Cunha 2003; Toledo et al. 1966).

However, despite their growing differences over time, Dobzhansky's work and support for colleagues in Brazil credits him in helping establish population genetics in Brazil, while also creating an important sphere of influence for the direction of study in Brazil and among affiliates in the region and beyond.

As James Crow wrote in 1987, by the 1950s both Dobzhansky and Muller found themselves at the center of questions related to radiation, genetics, and risk. Muller and Dobzhansky served together on the National Academy of Sciences Committee on the Biological Effects of Atomic Radiation (BEAR), which met several times during the mid-1950s and issued its report in 1956 (Crow 1987: 370). According to Crow, the major disagreement on the committee was whether to use the Haldane-Muller genetic load argument to arrive at a risk estimate. Many on the committee (and I quote here) "did not want to measure the impact of mutation in terms of fitness: equating human welfare, now and in the future, to Darwinian fitness seemed simplified to the point of being misleading. Muller recognized this difficulty but could think of no other way to estimate the total impact, extending into the far future, from mutation at all loci" (Crow 1987: 370-371). Eventually, the report contained a compromise that included an argument recognizing genetic load, but not exclusively. Dobzhansky and Muller could both sign on to the report, but some differences between them would persist, differences that Crow evaluates decades later, after extensive studies had been made in vertebrates, invertebrates, and plants regarding average heterozygosities—the quality of having different alleles for a particular trait.

Crow considers that neither Muller or Dobzhansky foresaw the possibility of a great deal of neutral variation, that Dobzhansky's ideas about overdominance did not hold up over time, and most significantly that:

> Muller's alarmist views of the hazards of radiation have prevailed rather than Dobzhansky's more moderate views. In my opinion, Muller was *too* effective in cautioning against radiation risks, with the result that the public now has an irrational fear of low-level radiation relative to other risks. The fear, I suppose, has resulted more from the assumption of no threshold for carcinogenic effects than from the dread of genetic effects. In any event, the battle that Muller wages was certainly won: the present standards for radiation safety are more stringent than even he dared advocate. (Crow 1987: 379).

These debates about radiation hazards originated among the preeminent Drosophilists of the 1950s and animated debates about radiation and genetics into the future. In the 1980s, for example, Rosalie Bertell (1985: 44–45) interpreted Muller's Drosophila research as predicting a reduction in the survival ability of the human species as several generations are exposed to ionizing radiation, a prediction that Bertell assumes was buried—or kept secret—by the Atomic Energy Commission in its consistent mission to underplay the harms caused by atomic weaponry and atomic energy.

I am not sure that—as Crow argues—Muller's alarmist views of the hazards of radiation have prevailed over Dobzhansky's more moderate views, but what is apparent here is that there is continuity between what exactly was being looked at in Drosophila—even in the more questionable experiments—and the later hardening of positions about radiation effects. We posit that animal studies—and here insect studies—may have been used to generate a form of "radiation effects denial," an outcome that some would contest. Many of the papers on insect radiobiology

were published prior to 1975. Insects in general, including Drosophila, are known to be incredibly resistant to radiation. Adult insects are at least 100 times less sensitive to the lethal effects of radiation than are vertebrates, and mammals are more radiosensitive than birds, fish, amphibians, or reptiles (O'Brien and Wolfe 1964). This is why the case of the mutant butterflies in Fukushima has been so disturbing.

Mutant Butterflies and Fukushima

In the animal kingdom, butterflies and moths belong to the Lepidoptera order. They are the second largest group of animals, surpassed only by beetles. In this they stand out, but so too for their incredible diversity, and their extensive use in research around the world (Goldsmith and Marec 2010). Lepidoptera species have fascinated humans for centuries (Russian novelist Vladimir Nabokov was a butterfly catcher), featuring prominently in literature and art throughout history and they continue to do so today. Their allure is no doubt partly attributed to their vividly colored wings, distinct life cycle stages, and rich biodiversity. Their economic value can't be overestimated. The moth *Bombyx mori*, for example, was domesticated for over five millennia in China, subjected to inbreeding and selective breeding, primarily in service to produce silk fibers, a trade that played a pivotal role in establishing trade networks spanning Europe, the Middle East, and Asia (Goldsmith and Wilkins 1995). As modern scientific approaches developed in the 18th century, so too did the scientific study of Lepidoptera. Since then, these insects have been used in various fields of research, from natural history and ecology to genetics and climate change.

As scientific subjects, interest in butterflies began during the age of European Exploration within the continuing throes of Enlightenment enthusiasm when nearly every insect or plant found across the planet was placed in a preservative liquid, sketched, dissected, and interned in vials. Early naturalists like Carl Linnaeus and Maria Sibylla Merian documented butterfly species, classifying, and illustrating them in their publications. Both amateur entomologists and professional researchers embarked on worldwide expeditions, collecting Lepidoptera specimens across Europe, Asia, South and North America, Australia, Africa, and the Pacific Islands. Some scientific expeditions, like those to the Congo, were specifically organized to collect, catalogue, and categorize various Lepidoptera species found in different regions of the world (Wolland et al. 1920). During this time, entomologists such as Jean-Henri Fabre and Henry Walter Bates made significant contributions to the intricacies of butterfly behavior and taxonomy. Their observations, particularly of mimicry, revealed how butterflies employ a variety of strategies to mimic other species, plants, and their surrounding environments.

The 19th century saw groundbreaking research on butterfly mimicry that influenced Charles Darwin's (1859) world shattering conclusions leading to *On the Origin of Species* and *Fertilisation of Orchids* in 1862. The latter detailed

the mechanisms of natural selection, particularly coevolution and the interaction between plants and insects. Additionally, the work of entomologist Fritz Müller expanded on evolutionary theory by focusing on mimicry: the evolution of an organism to resemble other species for protection against predators. Because Lepidoptera are believed to have evolved alongside flowering plants, they became central to the study of coevolution (Goldsmith and Marec 2010). This coevolutionary relationship demonstrates how entirely different biological groups—insects and plants—have evolved together, influencing each other's adaptations and survival strategies. The scientific focus on mimicry and coevolution highlights the historical significance of butterflies in evolutionary theory, establishing them as subjects of research in various fields, including in radiation studies.

With the development of the study of genetics and inheritance in the early 20th century, research on Lepidoptera expanded. Early studies focused on mimicry, breeding (Doncaster 1907), British "races" of butterflies (Verity 1919), melanism, or the darkening of wing pigment (Harrison 1920), inheritance of wing color (Onslow 1921), and geographical distribution of butterflies according to type (Kano 1931). The pioneering geneticist Alfred Russel Wallace, known as the "father of zoogeography," conducted breeding experiments involving butterflies and moths to gain insights into trait inheritance (DeMers 2017). Wallace showed, for example, that certain traits in butterflies, such as wing color and patterns, exhibit a significant degree of heritability. These findings implied that the diversity of butterfly wing colors and patterns were the result of genetic factors passed down from one generation to the next. Throughout the years, the utility of butterflies increased to a systems approach in environmental analysis with scientists employing them as ecological indicators, monitoring their populations and behaviors to help assess ecosystem health and the impacts of environmental transformations, including climate induced shifts in distribution. Today, butterflies often act as flagship species for conservation and biodiversity.[4] For example, conservation initiatives that focus on preserving butterfly habitats often result in the protection of various other species that share these ecosystems (New et al. 1995). Understanding butterfly populations allowed scientists to gauge the overall well-being of ecosystems. The impact of nuclear weapons testing and the expansion of the nuclear power industry in the mid-20th century on the environment, meant that butterflies could be used as indicators of radioactive contamination.

The history of ionizing radiation research on butterflies began in the 1940s with the expanding use of nuclear

[4] Throughout history, three primary research interests have driven the study of butterfly and moth species as a biological model system: evolutionary studies, endocrinology, and genetics (Goldsmith and Wilkins 1995). Lepidoptera, owing to their relatively large body size, have been favored biological model systems for the exploration of endocrinology and biochemistry. Their suitability for surgical manipulations, enabled by their ample body size, facilitated early research on how hormones regulate the lives of all insects. Subsequent studies in endocrinology and biochemistry within Lepidoptera species revolved around the need to control these insects as agricultural pests.

technologies and the nagging need to understand the biological effects of ionizing radiation on wildlife and ecosystems, as well as potential implications for human health (Michener 1942). Some of the earliest studies on radiation effects included collecting butterflies in Hiroshima and Nagasaki and at Brookhaven National Laboratory, New York among others (Congress of the United States 1959). The goal in these studies was to investigate the ecological impact of radiation exposure on insects (Ayres 1963). The findings indicated that butterflies had minimal adverse effects from radiation, with limited genetic damage. After the Chornobyl, and later Fukushima nuclear accidents, scientists were especially interested by what butterfly genetics might reveal (as well as other insects and mammals) about life in or near areas affected by nuclear fallout in assessing the impact of radiation on local ecosystems (Møller and Mousseau 2006; Mousseau and Møller 2014). This work examined the genetic and physiological effects of radiation, its implications for population dynamics, and how it influenced various life stages of these insects. Anders Møller and Timothy Mousseau's (2006) genetic studies of wild insect populations in Chornobyl, including butterflies, have already demonstrated significant genetic, physiological, developmental, and fitness effects stemming from exposure to radioactive contaminants. But it is the Fukushima accident and the mutant butterflies found there that spawned a heated debate about radiation effects (yet again). Indeed, butterflies have often been referred to as a canary in the coal mine, meaning that their sensitivity to habitat loss, invasive species, and land management are purported to tell us what our metaphorical oxygen readings are.

On March 11, 2011, the Fukushima Daiichi Nuclear Power Plant disaster marked the first major nuclear catastrophe since Chornobyl. Triggered by a 9.0 magnitude Tohoku earthquake and subsequent 45-foot tsunami waves, several reactors at the plant were severely damaged. Three of these reactors experienced meltdowns, causing what is only an estimable release of toxic radioactive elements into the atmosphere. To prevent further explosions, the reactors were deliberately vented, dispersing yet more radioactive particles. The precise extent of radiation release remains unclear, as does the number of people exposed to ionizing radiation and the potential long-term health consequences of such exposures.

The research on [Fukushima's] butterflies not only showed the presence of inherited genetic damage but also highlighted that those abnormalities and mutations persisted and even got worse in the offspring of exposed butterflies (second and third generation).

The events at Fukushima certainly provided a new vantage point and source of motivation to examine long-term health consequences. Shortly after, in August 2012, Joji Otaki, a professor at Ryukyu University in Okinawa, published a study (together with his colleagues) in *Nature's* online journal *Scientific Reports*, titled "The Biological Impacts of the Fukushima Nuclear Accident on the Pale Grass Blue Butterfly." The study revealed one of the more

disturbing consequences of the Fukushima disaster: the emergence of mutant butterflies in the vicinity of the damaged nuclear plant (Hiyama et al., 2012). The Japanese study forms part of a growing yet contested body of scientific literature linking chronic low-level radiation exposure to intergenerational genetic damage. The study emerged shortly after a Stanford University report estimated that the global health impacts of the Fukushima nuclear accident could lead to thousands of cancer mortalities and morbidities worldwide (Hoeve and Jacobson 2012). These findings have raised concerns both among scientists and those who faced exposure in the days and weeks following the accident. The research on butterflies not only showed the presence of inherited genetic damage but also highlighted that those abnormalities and mutations persisted and even got worse in the offspring of exposed butterflies (second and third generation). This groundbreaking study was the first to systematically illustrate the *accumulation* of genetic mutations across multiple generations. Although our understanding of butterfly recovery remains unclear, the scientific consensus is that insects are especially resistant to radiation. According to biologist and expert on radiation induced genetic mutations in animals, Timothy Mousseau, mutant genes with negative effects are expected to diminish over time as carriers become less able to survive and reproduce (Mousseau 2024, email correspondence). The speed of this purging process depends on factors such as the mutation's fitness effect, its dominance, and the effective population size. Dominant mutations are removed quickly, while additive mutations take longer, creating a mutation-selection balance. Recessive mutations can persist for generations, as seen in diseases like Tay-Sachs. Larger populations experience slower selection, allowing mutations of small effects to endure. Despite differences in chromosome numbers, fruit flies and butterflies operate similarly in mutation-selection balance.

The Okinawa research team's profound observation about mutant butterflies long after the initial accident at Fukushima contradicted common scientific knowledge about insect resistance. They found that the negative radiological effects seemed to manifest across generations, transmitted from parent to offspring. Their experiment exposed healthy butterflies to low dose ionizing radiation in a controlled laboratory environment, comparing those collected near Fukushima to those from other regions of Japan. In May 2011, the researchers collected adult butterflies in Fukushima and surrounding regions. Two months prior, at the time of the disaster, these individuals were in the larval stage, surviving underground during winter months (Foote 2013). These butterflies (with an adult lifespan of one week), what we understand as the first generation, exhibited physical abnormalities (deformed legs, broken antennae, and wrinkled wings) at a rate of 12% higher than the control group. The second and third generations saw mutation rates of 18% and then 34%, suggesting a direct correlation between genetic mutations and their inheritance. As time is one of the key factors in radiation research, along with dose, the study began to show more disconcerting revelations about butterflies as the months (and generations: F1, F2, F3, etc.) proceeded. When the scientists collected 240 butterflies in September 2011, months after the accident, they

discovered more pronounced and widespread abnormalities in 38.5% of the population. Since adult butterflies have a lifespan of only one week, it was evident that the mutations were not due to prolonged radiation exposure (see Foote 2013). This indicates that radiation is causing mutations to the germline as well as somatic cells, with these abnormalities being inherited.

These were provocative results and the study attracted considerable attention both inside and outside Japan, some of it decidedly negative, with many criticizing the design and the conclusions of the study (Otaki and Taira 2018). The criticism, coming from the United Nations Scientific Committee on the Effects of Atomic Radiation (UNSCEAR 2014), echoed its earlier assessment of the Chornobyl disaster, declaring that radiation effects on "non-human biota" in highly contaminated areas are "unclear" and are "insignificant" in less contaminated areas. The findings expressed several lines of argument, but were all based on the same question: can we really be sure the abnormalities were caused by radiation fallout from the Fukushima plant? After all, studies suggest that insects are relatively radiation resistant, but the butterfly was not, which surprised the Japanese researchers (see Oskin 2012; Raines et al. 2020). Given the fact that so much of our understanding of radiation effects has been done in the context of Drosophila, one can by now imagine the upset that the butterfly research has caused. The controversy surrounding the study highlights the complex and debated nature of interpreting radiation effects on insects, particularly in areas of different contamination levels.

After Fukushima, the UNSCEAR published a report summarizing and evaluating research on the biological effects of the nuclear accident from their viewpoint, discussing the mutant butterfly study in detail (UNSCEAR 2014; see also UNSCEAR 2015; UNSCEAR 2016). The 2014 UNSCEAR (83) reports, for example, that:

> the relationship between exposure and effect has not been unequivocally established in these studies. Furthermore, the observations are not consistent with the Committee's assessment and suggest that further analysis is needed to establish whether radiation exposure was an important factor, among many others, including the impact of the tsunami itself, in causing the environmental effects observed.

The 2016 UNSCEAR maintains that these results are not compatible and consistent with the conventional understanding of radiation biology. It is not compatible because the results, derived primarily from laboratory experiments involving external irradiation, don't show any harmful biological effects associated with low-dose exposure. But if the radiation damage produces more lethal genes, as the butterfly study seems to suggest, the butterfly may really be a canary in the proverbial coal mine, unlike other insects. The Fukushima study is currently challenging established paradigms in radiation biology and may require a reevaluation of the potential genetic impacts of low-dose radiation exposure on different species. After all, the results suggest that the area around Fukushima is dangerous beyond current levels of understanding, perhaps even uninhabitable for humans.

Perhaps it is this butterfly/scientific uncertainty, together with the political and economic implications, that is contributing to the controversy. Regardless, thus far, no peer-reviewed scientific study has definitively shown that humans experience the same outcomes as butterflies. The prevailing consensus among scientists is that humans are more resistant to radiation's effects than butterflies (UNSCEAR 2014), a point consistent with some, but not all our understandings of radiation biology. Drosophila, for example, can be maximally irradiated and then bred and then come back to some stasis. What happens to the population of butterflies remains uncertain.

The butterfly studies nevertheless carry alarming implications for our understanding of radiation's biological effects. They suggest that, despite challenges in extrapolating data from animals to humans, people might also be susceptible to transmitting damaged heritable germ-line DNA to future generations, a finding that the ABCC was reluctant to make (Goldstein and Stawkowski 2015). As Hiyama et al. (2012:8) note, "heritable germ-line genetic damage caused by low-dose exposure due to radioactive contamination in a species of butterfly has invaluable implications for the possible future effects of radiation on animals." Otaki warned it was too soon to jump to conclusions, saying his team's results on Fukushima butterflies could not be directly applied to other species, including humans. It is interesting that we cannot jump to any conclusions about humans based on butterflies, but we can see from the Drosophila work discussed in the opening of this paper, that the transition from insect to human genetics occurred with great frequency and the assemblage of knowledge learned in Drosophila work was brought to bear on our understanding of human radiation biology. Compared to Drosophila, the butterfly may indeed be more sensitive and alert us sooner to consider what the long-term effects of radiation exposure might be. It seems that both the population biologists and the UNSCEAR reports assume that the mutations will disappear over time and reach a new stasis, rather than increasing as they do in these recent studies of butterflies in Fukushima.

Conclusions

Several issues are gaining clarity in looking at insects. In other approaches that our work has taken—both collectively and individually—where we have tried to understand the contemporary foundation upon which the pronouncements about radiation risk are made, we began to see the outlines of numerous debates and a context much larger than we anticipated.

In our last joint paper in 2015, we contrasted the perspectives of two geneticists, James V. Neel from the U.S. and Yuri Dubrova, originally from Kyiv, Ukraine but later a migrant to the UK. Our goal in that work was to try to understand the assertions of the Atomic Bomb Casualty Commission. In that work, too, while the scientific uncertainty was central, we also considered the broader context of their scientific training and other alliances.

James Neel's status and scientific reputation, we wrote, "gave him the opportunity to help establish radiation safety standards for nuclear workers and the public. Through the interdependency of funding and prestige, they also enabled him and his colleagues to build the large-scale statistical models in population and epidemiological genetics that have become the gold standard for research, while other scientific methods and approaches were dismissed as substandard" (Goldstein and Stawkowski 2015: 92). In this essay, we take the construction of these quite durable findings from a different perspective on the research conducted among atomic bomb survivors since 1950 and the many subsequent reports addressing the risks associated with low dose ionizing radiation, which are renewed in every cycle of UNSCEAR work. The angle we take here has us approaching these epistemological questions differently with a specific focus on insects. We hope that this different lens can help us further configure the endurance and forms of radiation risk knowledge.

One of the things that has become clear to us here is the foundational role of model organisms in the field of human genetics. Among these organisms, Drosophila is an important actor in this production of knowledge. This tiny creature has played an important role in our understanding of population genetics. Population biology and its surrounding disciplines are also key here. In the pre-DNA world described in the Drosophila research in Brazil, the measurement of all things was supposed to lead to knowledge about populations—what they looked like, how they developed, what changes an irradiated laboratory fly versus a naturally occurring one might produce in that population—all to find out what the future populations of flies (and ultimately humans) would look like. It became common knowledge that insects could be exposed to a great deal of radiation and could survive, and that subsequent generations would not see too much destabilization. This helps to explain why H.J. Muller's simultaneous belief that irradiated flies were no more lethal than mutant flies in nature, a finding that seems contradictory to his lifelong quest to secure an understanding of the dangers of radiation. Crow, however, found Muller's worry to be overwrought, and the endless reports from UNSCEAR declaring that the risks to human populations are minimal—at least from our reading—hold to the core principles established by the original ABCC research directed by James V. Neel. While we are not entirely certain whether these principles are too stringent, what we do see is a tendency to both dismiss and downplay radiation concerns and envision a future built on a sense of resiliency for us all.

That is, until we get to Fukushima and the butterfly. In this case, we find an insect that ought to be able to handle the radiation effects of the nuclear meltdown in the region, but instead, shows alarming signs of mutation and intergenerational damage. The studies of mutant butterflies from Fukushima serve as a reminder of the risks associated with radiation exposure. The research on butterflies not only revealed the presence of inherited genetic damage but also showed its exacerbation in the second and third generation in these insects. We are uncertain

what this means for the recovery of the butterfly or for that matter, us humans. The implications of these findings are vast, even if direct relevance to human health and genetics remains inexact. We are left with lingering questions about what it might all mean.

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