Trends in Ecology & Evolution

Volume 31 Number 4 April 2016 ISSN 0169-5347

Thirty Years after Chernobyl; Are Organisms Adapting?

CellPress

April 2016 Volume 31, Issue 4

This year marks 30 years since the explosion at the Chernobyl nuclear reactor in Ukraine. This has provided an opportunity to study the effects on organisms of radiation levels higher than the usual background but still low enough to allow survival and reproduction. On pp. 281–289 of this issue, Anders Møller and Tim Mousseau review evidence of adaptation by organisms to this level of ionising radiation. They find the evidence so far is a long way from being convincing. The cover shows white storks (*Ciconia ciconia*) nesting on top of a water tower at an abandoned farm near Chernobyl. Photo: Tim Mousseau.



Review Are Organisms Adapting to Ionizing Radiation at Chernobyl?

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Numerous organisms have shown an ability to survive and reproduce under lowdose ionizing radiation arising from natural background radiation or from nuclear accidents. In a literature review, we found a total of 17 supposed cases of adaptation, mostly based on common garden experiments with organisms only deriving from typically two or three sampling locations. We only found one experimental study showing evidence of improved resistance to radiation. Finally, we examined studies for the presence of hormesis (i.e., superior fitness at low levels of radiation compared with controls and high levels of radiation), but found no evidence to support its existence. We conclude that rigorous experiments based on extensive sampling from multiple sites are required.

Chernobyl, Fukushima, and Resistance to Ionizing Radiation

The year 2016 demarks the 5th and 30th anniversaries of the Fukushima and Chernobyl nuclear disasters, respectively, and there is growing public and scientific interest concerning the impacts of such accidents on natural systems, given the likelihood of additional accidents in the future [1]. In addition, there is considerable heterogeneity in natural levels of ionizing background radiation across the globe, with significant negative effects on numerous organisms, including humans [2]. Hence, it is not surprising that not only many microorganisms [3-5], but also eukaryotes, have evolved an ability to tolerate, resist, or even benefit from such radiation [2]. Furthermore, there is reason to believe that adaptation to other stressors, such as ultraviolet (UV) radiation, can facilitate the evolution of resistance to ionizing radiation. Thus, microorganisms that do well in Chernobyl are also those that do well on sunlight-exposed surfaces elsewhere ([6] S. Jenkinson et al., unpublished data, 2016). Therefore, adaptation to ionizing radiation can arise either from an increase in the frequency of alleles that were already present before the accident at Chernobyl, due to adaptation to other stressors, or de novo from mutations. There is every reason to expect evolution of resistance to radiation, even among organisms that have only been irradiated since recent nuclear accidents, such as that at Chernobyl in 1986, because the intervening period of 30 years is sufficient for changes in phenotype in standard selection experiments for all organisms apart from those with the longest generation times. Such effects of radiation will depend on exposure to radionuclides, as reflected by internal dose (Box 1). In the past, novel radioactive sources, such as those caused by asteroids and eruption of volcanoes, will have caused significant levels of deleterious mutations resulting in reduced viability and, thus, preventing large fractions of populations from evolving significant levels of resistance to radiation. There is also reason to believe that populations of animals were exposed to such a high level of radiation that it could have reduced their population size and imposed significant directional selection (Box 2).

lonizing radiation directly increases the frequency of chromosome breakage, although it also has indirect effects via oxidative stress that causes DNA mutations (Box 3). Since mutations ultimately are the source of novel genetic variants, ionizing radiation could contribute to evolution

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In total,17 studies have suggested that they have demonstrated adaptation to ionizing radiation from Chernobyl, while in fact only two of these fulfill the criteria for evolutionary adaptation.

Lack of evidence of adaptation mainly derived from the lack of replication and of rigorous experimental design.

There was no evidence of hormesis, with organisms at low levels of radiation performing better than at typical background radiation in uncontaminated areas

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Box 1. Dose Rates and Populations

In the first study of its sort, Gamier-Laplace *et al.* [58] calculated dose rates for 57 species of birds (almost 7000 individuals) living in Fukushima following the nuclear disaster of 12 March, 2011. Doses were calculated based on radiological conditions at the point of observation and corrected for by including ecological and life-history attributes of a given species. Dose was used to predict the total number of birds, while statistically controlling for potentially confounding environmental variables (e.g., habitat type, elevation, presence of water bodies, ambient meteorological conditions, and time of day). Total dose was found to be a strong predictor of abundances (P < 0.0001), which showed a proportional decline with increasing doses with no indications of a threshold or intermediate optimum. Overall, the $ED_{50\%}$ (i.e., the total absorbed dose causing a 50% reduction in the total number of birds) was estimated to be 0.55 Gy. This value can be compared with a value of 0.05 Gy as background radiation in uncontaminated areas around Fukushima before the accident in 2011 [59] Figure I.



Figure I. Log Logistic Model Fitted to Randomly Predicted Total Number of Birds Derived from a Global General Linear Mixed model, and Its ED_{50%} Prediction and Associated 95% Confidence Interval ED_{50%} Is the Total Absorbed Dose Causing a 50% Reduction in the Total Number of Birds. Adapted from [58].

by speeding up evolutionary change. For example, radiation was used as early as 1925 to induce novel variants for plant breeding and agriculture [7,8], and the genes encoding such variants were subsequently selected in selection experiments. Some scientists have even speculated that adaptation to low-dose radiation *per se* could facilitate evolution. These hypothetical effects also relate to the notion of radiation hormesis, which suggests that low doses can have beneficial effects on organisms, for example via induced DNA repair [9–11]. Here, we not only review the literature on the evolution of resistance to ionizing radiation, but also address the potential underlying mechanisms and experimental designs used to assess the genetic and environmental effects on adaptation to radiation.

Adaptation to Radiation

Several studies have concluded that there is evidence of adaptation to low-dose radiation at Chernobyl (Table 1). These range from proteomic analyses of plants showing changes in the amounts of proteins produced [12,13] and studies of DNA methylation that affect whether a gene is expressed [17] to other physiological mechanisms [12,14]. There is also evidence consistent with adaptation through the intracellular antioxidant glutathione, showing that some species of birds that do best under conditions of ionizing radiation have evolved the highest levels of glutathione [15]. Perhaps the most clear-cut evidence for adaptations concerns resistance to radioactivity in generalist bacteria, which are widely distributed across Europe [16].

Box 2. Are There Effects of Radiation on Populations?

A recent study [60] suggested that some large mammals, particularly those normally under significant hunting pressure, were thriving inside the Belarusian part of the Chernobyl Exclusion Zone (Figure I). The data presented only showed a partial rebound of some mammals following the initial highly deleterious effects of the disaster, while the data for contemporary population densities were primarily collected in regions of relatively low radioactivity while ignoring large regions of intermediate and high radiation levels in both Belarus and Ukraine (e.g., the region in and around the so-called 'Red Forest'), thus lowering the statistical power of any potential tests for radiation effects. In addition, there was no attempt to estimate the internal dose of the species concerned. Furthermore, attempts made to correct for confounding factors, such as habitat type or human habitation, were inadequate and conducted at a geographic scale likely to obscure any relations with radiation effects, which are highly heterogeneous. Finally, no rigorous attempt was made to compare suggested population trends to those from other wildlife refuges in Europe. Overall, the reported findings do not address the issue of whether populations have adapted to the radiological conditions found inside the Chernobyl zone.



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Figure I. The Number of Track Counts Of Elk (A) and Wolves (B) in the Belarusian Part of the Chernobyl Exclusion Zone. Data points represent annual estimates. Adapted from [60].

Adaptation is a biological concept that has many different meanings in fields as diverse as evolution, physiology, and neuroscience [17-20]. Most biologists consider that, for evolutionary adaptation to apply, there should be evidence of an increase in fitness across all environments, and that changes in phenotype over space (selection and the increase in fitness) should be associated with a change in genotype frequency [20]. Thus, an adaptation sensu stricto requires that there is at least a local or even a global fitness optimum. This definition also implies that pre-adaptations that have evolved in a context other than the focal phenomenon do not qualify as evolutionary adaptations [21]. By contrast, physiologists consider design features of phenotypes that facilitate the performance of even a single individual in a given environment to suffice as physiological adaptations [22]. Thus, physiological adaptation reflects the extent to which an individual performs optimally in a given environment, therefore focusing on acclimation to the specific environment and the required physiological responses [22]. Such physiological mechanisms can be inherited through epigenetics (i.e., mechanisms, such as methylation, which affect whether a specific nucleotide is expressed, but not the actual nucleotide at a specific locus) that can apply even across generations. Adaptation in neuroscience implies the temporal change in response of a sensory system to a specific stimulus. However, here, we only consider evolutionary adaptations. Irrespective of the definition of adaptation, there is an explicit or implicit assumption that there are one or more environmental gradients that characterize the extent of optimality of the environment.

The process of adaptation by natural selection requires several key elements. First, there must be phenotypic variation among individuals within a population in their ability to perform in response to the selective agent (in this case radiation). Second, there must be a genetic basis underlying any observed variation in performance. Third, variation in performance must be heritable; that is, offspring must resemble parents as a consequence of inheriting the genetic factors responsible for variation in performance (e.g., [20]).

It seems likely that all organisms currently living have adapted to some degree to the consequences of ionizing radiation, given the near-ubiquity of past or current elevated background radiation on the planet, which in the past was even higher than at present (e.g., [2]). However, it

Box 3. Effects of Radiation from Chernobyl on Mutations

Given past and present interest in the long-term effects of ionizing radiation on genetic materials (i.e., DNA), it is perhaps surprising that there have been relatively few studies directly addressing this question and few attempts to review and synthesize the current state of knowledge concerning impacts on natural populations. Møller and Mousseau [61] used a meta-analysis of 45 published studies covering 30 different species, including humans, to investigate the impacts of Chernobyl-derived radiation on measures of genetic damage. The overall conclusion was that there are large effects of radioactivity stemming from the Chernobyl accident on measures of genetic damage with an overall effect size of E = 0.67 (95% confidence interval = 0.59 – 0.73, N = 151 estimates) accounting for 44.3% of the variance in an unstructured random effects model. Of special relevance here, effect size did not change with time since the accident of the study, thus providing no systematic evidence for evolved adaptation to radiation. The effects of radiation on genetic damage varied among taxa, with plants showing larger effects than animals. Humans were shown to have intermediate sensitivity to radiation as measured by mutations, when compared with other taxa (Figure I).



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Figure I. Cumulative Distribution of Effect Sizes Weighted by Sample Size of Mutation Rates at Chernobyl Ranked from the Weakest Negative Effects to the Strongest Positive Effects. Each bar and its 95% confidence interval (CI) represents one effect size. Effects sizes not overlapping with the vertical line at zero differ significantly from zero. The mean effect size of 1.09 was one of the largest in any biological meta-analyses. Adapted from [61].

has been often suggested that terrestrial life did not arise on Earth until atmospheric oxygen levels had risen sufficiently to block the damaging effects of UV radiation [23,24], which implies a limit or constraint on the ability of populations to adapt to mutagenic environments.

Without the ability to repair the damage caused directly and indirectly by ionizing radiation to not only genetic materials, but also proteins, including cell surface proteins, it seems likely that life would not exist on this planet, at least in regions where radiation and other mutagens are found. DNA repair has evolved in response to many physiological stressors that cause genetic damage [25,26], but mechanisms that eliminate proteins that have been damaged have resulted in the evolution of other mechanisms. Such repair mechanisms not only affecting damaged DNA, but also causing elimination of damaged proteins, can pre-adapt some species to higher ionizing radiation levels. Defective DNA repair abilities are often associated with disease, including cancer [27–29].

Given the likelihood of sustained directional selection for improved DNA repair ability and the reduction of radiation-induced cellular damage since the beginning of life on Earth, evolutionary theory would suggest that little adaptive genetic variation in such repair mechanisms would presently exist in most populations. This is because, for simple Mendelian traits, beneficial mutations are rapidly fixed, deleterious mutations generally are eliminated, and only neutral mutations persist in most population unless eliminated via population bottlenecks or founder effects [30]. Fundamentally, this relatively simple axiom of population genetics is the reason that radiation hormesis is unlikely to exist, at least with respect to genetic damage.

lable 1. Studies Investigatir	ng Adaptation to Hadiation tro	om Chernobyl						
Species	Response Variable	Experimental Design	Sample Size	Optimal Radiation Level	Hormesis	Evidence for Adaptation	Comments	Refs
Bacillus pumilus	Resistance to radiation	Common garden	Four sites	Yes	No	Yes		[16]
Staphylococcus aureus	Resistance to radiation	Common garden	Four sites	Yes	No	Yes		[16]
Arabidopsis thaliana	Sensitivity to mutagens	Transplant experiment	Three sites	°Z	No	Yes?	High-contamination plants more resistant to two mutagens	[12]
	Recombination rates	Transplant experiment	Three sites	0 Z	°Z	Yes?	Lower recombination rates in plants from contaminated areas could be caused by mechanisms other than adaptation	[12]
	Methylation	Transplant experiment	Three sites	No	No	No		[13]
Pinus sylvestris	Methylation	Field samples	Three sites		No	No		[13]
	Number of aberrant cells in root meristems	Field samples		No	No	No		[62]
Betula verrucosa	DNA repair	Field samples	Three sites	Yes	No	Yes?		[48]
Oenothera biennis	Germination under stress	Field samples	Three sites	Yes	No	Yes		[48]
Glycine max	Proteome	Seeds sown in two different plots	Two sites	°Z	No	°Z	Smaller size of seeds could be pathological response; 64 of 698 (9.2%) proteins differed	[49]
	Proteome	Seeds sown in two different plots	Two sites	°Z	No	°Z	Smaller seeds and reduced germination could be pathological response	[14]
Linum usitatissimum	Proteome	Seeds sown in two different plots	Two sites	°Z	°Z	°Z	Smaller seeds and reduced germination could be pathological response; 35 of 720 (4.9%) proteins differed	[63]
Chorthippus albomarginatus	Morphology and development	Common garden	Six sites	No	No	No		[54]
	DNA damage	Common garden	Six sites	°Z	°Z	°Z		S. Jenkinson <i>et al.</i> , unpublished data, 2016
Birds	GSH	Field samples	Eight sites	No		Yes?		[15]
Voles and vole-moles		Field samples	ن	2	No	No		[64]
Clethrionomys glareolus	Resistance to radiation	Field samples	ć	No	No	No		[65]
^a Optimal radiation level indicates levels of radiation compared w	s whether the organism performed with uncontaminated controls), evi	better at an intermediate level of radiation	than at lower o	or at higher re	adiation levels	; hormesis indic	ates whether the organism perform	ned better a low

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Current explorations of mutation-selection balance theory suggest that, for natural populations of finite sizes of less than a few thousand individuals, the addition of a small number of deleterious mutations can tilt a population towards local extinction [31]. This is because many populations exist in a balanced state that reflects ongoing adaptation to local environmental conditions and the fitness costs of constant immigration of individuals (maladaptive genotypes) that are not optimally adapted to local conditions. If the environment changes quicker than the population can adapt, it will go extinct. Likewise, genetic load due to the addition of deleterious mutations via radiation effects can tip a local population towards extinction. Population size, inbreeding effects, immigration rates, and breeding systems are likely to influence this process, but the ultimate outcome for finite populations with limited immigration is likely to be extinction [30].

Selection and the Microevolution of Superior Phenotypes

Although several studies of plants and animals at Chernobyl have shown effects of intense selection, resulting in the elimination of inferior phenotypes (i.e., purifying selection, which eliminates alleles with deleterious effects) [32-45], we are unaware of even a single study showing directional response for improved performance within populations that have been subject to intense selection at Chernobyl or elsewhere (Table 1). This is perhaps surprising given that most traits not only show some degree of heritable genetic variation [46], but will also respond when selection is applied (e.g., artificial selection for desirable traits can lead to population responses greater than several standard deviations in just a few generations [47]). It is perhaps telling that response to selection for increased radiation resistance appears to be rare, perhaps reflecting a long history of selection that has eroded standing genetic variation for this trait. Boubriak et al. [48] showed enhanced DNA repair in a single sample of pollen from silver birch Betula verrucosa, although random factors can account for such an effect. In part, this absence of studies stems from the general prediction and observation that most, if not all, novel mutations are either neutral or slightly deleterious with respect to fitness; the spontaneous generation of a beneficial mutation is believed to be a rare event that, when it occurs, proceeds to fixation at a rapid pace. Geraskin et al. [49] showed in a 6-year study that there was no change in the number of aberrant cells in root meristems of seeds exposed to a novel acute dose of radiation. This lack of temporal change in the number of aberrant cells suggests, for this system, that there is an absence of adaptation to ionizing radiation.

Are there any studies showing adaptation to radiation (Table 1)? Ruiz-González et al. [16] showed for two common strains of bacteria from feathers of barn swallows Hirundo rustica from three study areas near Chernobyl and from Denmark (an uncontaminated control area) that bacteria originating from areas with intermediate radiation exposure performed better in terms of resistance to an external radiation source in a common garden environment than did bacteria from the control areas or the most irradiated areas. These bacteria on the plumage of swallows are exposed to high radiation levels from the radionuclides in the soil used for the construction of nests. The common garden experiments suggested that bacteria performed the best at an intermediate radiation level. It is perhaps surprising that there was no evidence of adaptation to high radiation levels, given the higher intensity of selection that exists in such environments. Explanations for this include the possibility that mechanisms associated with adaptation to intermediate radiation levels are different from those required to survive in highly radioactive environments and that there is no genetically based variation in resistance to high mortality. Likewise, adaptation to low levels of radiation is unlikely because selection for resistance is likely to be lower [47]. Another explanation might be that costs of resistance (e.g., reduced replication rates) exceed the benefits of increased survival, with the net effect that the contribution of these variants to future generations will be negligible. In addition, gene flow among populations inhabiting heterogeneous environments can stymy evolutionary responses [50] and has been found to limit population responses to selection in the face of climate change (e.g., [51]).

Radiation hormesis posits that individuals perform better when conditioned by exposure to a low dose of radiation, implying that there is a nonlinear relation between fitness and radiation [9–11]. We are unaware of any studies showing experimental evidence of radiation hormesis effects under field conditions in whole-organism settings. The common garden experiment on bacteria, which was crossed with an irradiation treatment, as discussed above [16], is also interesting from a hormesis perspective because the bacteria did not show superior performance when at low levels of radiation, suggesting a cost to adaptive mechanisms in the absence of radiation. Hence, we conclude that there are no explicit tests demonstrating radiation hormesis effects for whole organisms under field conditions.

Experimental Designs

17 studies had samples from a single contaminated site and a single control site, or a maximum of three sites differing in level of radioactivity. The use of samples from individuals from each such site is effectively pseudoreplication [52]; that is, the use of multiple observations from a single site as if they are statistically independent, despite such observations being dependent because they share a common environment. Thus, no robust conclusions can be drawn from such data. However, even multiple studies each based on two sites can be used to draw general conclusions in meta-analyses, in which effect size estimates are weighted by sample size to achieve an overall effect size estimate across studies [33]. Such a meta-analysis is equal to coin flipping, with the null expectation being that an equal number of studies go in each of the two directions [33].

There are several standard designs that can be used to make rigorous tests of adaptation to radiation. The prime design used to make inferences about the effects of environment of origin and the environment of rearing is reciprocal transplants between contaminated and uncontaminated sites [53]. In this experimental design, individuals of two (or more) common origins (one contaminated and one noncontaminated) are both reared not only in their home environment, but also in the 'other' environment, allowing for both populations to be reared under both levels of contamination. This allows not only for the comparison of the phenotype of individuals reared 'at home' or away from their native environment, but also for a rigorous test of the effect of an interaction between environments of origin and rearing. Surprisingly, we are unaware of any such approaches in the study of effects of radiation.

Another standard design that is less rigorous is the common garden experiment, where individuals from multiple environments varying in their level of exposure to radiation in previous generations are reared together in a benign environment. If the effect of radiation is maintained in the common garden in the current, but also in the subsequent two generations, we can infer that the differences have a genetic basis and are unlikely to be due to epigenetic or maternal effects. This approach has been used in grasshoppers [54], although the evidence of phenotypic differences being related to radiation was negligible. Ruiz-González *et al.* [16] used common garden experiments on two strains of bacteria of the species *Bacillus pumilus* and *Staphylococcus aureus* to test for increased performance under elevated levels of radiation. Common garden experiments have also been done by rearing plants from seeds collected at different radiation levels at Chernobyl in an uncontaminated greenhouse.

Yet another design is the rearing or maintenance of standard organisms in environments differing in level of radiation. We are only aware of one study using the blue mouse *Mus domesticus* assay to quantify somatic mutations in the Red Forest [55]. In such experiments, it is crucial that the rearing conditions do not interfere with the outcome by the provisioning of high levels of antioxidants in the diet, which can reduce or eliminate DNA damage.

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These designs are useful for demonstrating likely adaptive responses to past selective environments (i.e., explaining the past), but they do not provide information in and of themselves concerning the mechanisms underlying any observed phenotypic variation; neither do they speak to the potential for future evolutionary responses. The ability to predict response to selection requires knowledge of the heritable basis of phenotypic variation with respect to resistance to radiation, which to our knowledge has never been addressed.

Concluding Remarks

Where to go from here? There is plenty of evidence for rapid evolutionary change in the face of a changing environment (e.g., [56,57]). Hence, there is every reason to expect that microevolutionary change can be demonstrated by studies at Chernobyl and Fukushima. We conclude that there is a need for investment in long-term ecological studies conducted within a genetic framework if we are to predict future responses to radiation exposure. Surprisingly, there are no whole-genome estimates of mutation rates caused by chronic radiation exposure despite 30 years having passed since the accident in Chernobyl. Likewise, there are no estimates of how chronic exposure to radiation lead to evolutionary changes in mutation rates (see Outstanding Questions).

Which organisms to study? We suggest that a variety of organisms, such as sexual versus asexual organisms, will be most informative. Such studies could benefit from analyses of the mechanisms of adaptation (i.e., DNA repair) and the costs of adaptation (i.e., trade-offs).

We have emphasized that not all designs are equally powerful and that some are nothing but classical examples of pseudoreplication. Reciprocal transplant experiments are the way forward because they allow for quantification of the extent of adaptation, the mechanisms involved, and the costs of adaptation.

Although hormesis is often purported to have a role in adaptation to radiation, we are unaware of even a single study demonstrating hormetic effects of ionizing radiation under field conditions. Again, this boils down to the question of how to make a rigorous test, with reciprocal transplant experiments being the way forward.

Acknowledaments

We are grateful for support from the CNRS (France), the Samuel Freeman Charitable Trust, The American Council of Learned Societies, and the College of Arts and Sciences at the University of South Carolina.

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Outstanding Questions

Whole-genome estimates of mutation rates caused by chronic radiation.

Estimates of how chronic exposure to radiation lead to evolutionary changes in mutation rates.

Reciprocal transplant experiments between irradiated and uncontaminated study plots to quantify environmental and genetic effects for adaptation to radiation.

Accumulation of mutations within individuals over time in contaminated and control areas.

Assessment of ecological factors responsible for differences in mutation accumulation and adaptation.

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