Biological consequences of Chernobyl: 20 years on

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The disaster at the Chernobyl nuclear power plant in 1986 released 80 petabecquerel of radioactive caesium, strontium, plutonium and other radioactive isotopes into the atmosphere, polluting 200 000 km² of land in Europe. As we discuss here, several studies have shown associations between high and low levels of radiation and the abundance, distribution, life history and mutation rates of plants and animals. However, this research is the consequence of investment by a few individuals rather than a concerted research effort by the international community, despite the fact that the effects of the disaster are continent-wide. A coordinated international research effort is therefore needed to further investigate the effects of the disaster, knowledge that could be beneficial if there are further nuclear accidents, including the threat of a ‘dirty bomb’.

Introduction

One of the four nuclear reactors of the Chernobyl nuclear power plant exploded on 26 April 1986 as a consequence of human errors owing to a temporary shutdown of the cooling system. The explosion transported vast amounts of radioactive material into the atmosphere, much of which was subsequently deposited not only in the immediate vicinity of the power plant in Ukraine, Russia and Belarus, but also over large parts of Europe and other continents (Figure 1). On this, the 20th anniversary of the worst environmental nuclear disaster in history, there is still much disagreement among government agencies, health professionals and scientists over the long-term effects of low-level nuclear contaminants. The official UN position [1] suggests that the consequences to human health are much lower than expected, the park-like appearance of the 2044.4 km² Chernobyl exclusion zone, with large mammals appearing to be increasing in numbers, suggests an ecosystem on the rebound. However, the UN report, and interpretations of it in the popular and scientific press (e.g. [2,3]), has generated an optimism that might be unfounded.

Here, we discuss the information available concerning the effects of the Chernobyl disaster on wild plant and animal populations, and also humans. It is our hope that this information will serve as a foundation for future studies investigating the long-term ecological and evolutionary repercussions of chronic exposure to low-level radioactive contaminants (low-level radiation has been defined as the dose below which it is not possible to detect adverse health effects, typically 1–20 rads). Given that the effects of the disaster were felt on a continent-wide scale but that research has generally been the result of investment by a few individuals, we also call for a coordinated international research effort to further investigate the environmental outcomes of the disaster.

A brief history of the Chernobyl event

On 26 April 1986, during a test of the ability of the Chernobyl nuclear power plant to generate power while undergoing an unplanned shutdown, safety systems were turned off, leading to an explosion and nuclear fire that burned for ten days, releasing between $9.35 \times 10^3$ petabecquerel (PBq) and $1.25 \times 10^4$ PBq of radionuclides into the atmosphere (by contrast, the Three Mile accident in Pennsylvania, USA on 27 March 1979 released just 0.5 terabecquerel). Although many of these radionuclides either dissipated or decayed within days (e.g. $^{131}$Iodine), $^{137}$Caesium ($^{137}$Cs) still persists in the environment even hundreds of kilometres from Chernobyl. Likewise, $^{90}$Strontium ($^{90}$Sr) and $^{239}P$Plutonium ($^{239}$Pu) isotopes are common within the exclusion zone. Given the 30, 29 and 24 000 yr half-lives of $^{137}$Cs, $^{90}$Sr and $^{239}$Pu, respectively, these contaminants are likely to be of significance for many years to come.

Physiological and genetic effects of radiation

Immediately following the accident at Chernobyl, humans exposed to high-level radiation suffered from acute radiation sickness, including dizziness, vomiting and fatigue [1]. The long-term physiological effects of immediate and later exposure have also shown changes in levels of antioxidants, immunity and hormones. Most of the long-term consequences of the Chernobyl disaster stem from the inhalation and ingestion of radionuclides generated by the explosion and nuclear fire (Box 1), in contrast to the effects that result from direct exposure to radiation from a nuclear blast. The genetic consequences of radiation exposure will depend on the received dose, dose rate and other indirect effects (Box 1).

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Antioxidant, immunity and hormone effects

Radiation can reduce levels of antioxidants, such as carotenoids and vitamins A and E, which are used for protecting DNA and other molecules from damage caused by free radicals [4–8]. Consistent with this prediction is the finding that barn swallows *Hirundo rustica* studied during 2000 from the most radiation-contaminated areas had significantly reduced amounts of carotenoids and vitamins A and E in blood and liver, compared with birds from control areas [9] (Box 2), although the level of radiation was low compared with previous studies of humans [4–8] (Box 3). These reductions were the best predictor of increased frequency of abnormal sperm from male barn swallows in such areas [9].

Antioxidants can have important consequences for immunity owing to their immunostimulating effects (reviewed in [10]). Studies of Chernobyl staff involved in cleaning-up immediately after the accident revealed impaired immune function compared with that of matched control individuals [11–13]. Likewise, barn swallows from Chernobyl had depressed levels of several types of leukocytes (e.g. heterophils and lymphocytes) and immunoglobulins, and reduced spleen mass compared with individuals from control areas [14], suggesting a reduced ability to raise an efficient immune response. The heterophil:lymphocyte ratio, which is an important physiological indicator of stress [15], was also elevated in barn swallows from Chernobyl compared with control individuals.

The elevated frequency of partial albinism in barn swallows, humans and other organisms from the Chernobyl region can also be linked to an antioxidant deficiency [16,17]. Normal plumage or skin colour is produced by the migration of melanocytes from the skin (so-called ‘melanoblasts’) to feathers; such migration can be disrupted or melanocytes can die prematurely owing to low concentrations of antioxidants in the skin, resulting in albinism. Mutations in genes encoding plumage colour can have a similar effect [17], as shown by the finding that feathers with melanin-based colour are paler in barn swallows from Chernobyl compared with those from individuals from control areas [14]. Surprisingly, to our knowledge,
Box 1. Radiation exposure, pathways and effects in animals

Pathways of exposure
There are several ways in which animals can be exposed to radiation. (i) Exposure by inhalation occurs as a result of breathing radioactive dust, smoke or gaseous radionuclides into the lungs, where radioactive particles often remain for a prolonged period. Such exposure is most relevant for α or β particle-emitting radionuclides (e.g., 239Pu or 137Cs and 89Sr, respectively) because of the possible prolonged exposure to the respiratory system. This is likely to be a major pathway of exposure for those animals affected by Chernobyl fallout. (ii) Exposure by ingestion occurs as a result of swallowing radionuclides. α and β emitters are again of greatest relevance owing to possible prolonged contact with the digestive system. Also, because Sr and Pu are readily absorbed, internal organs and tissues are also at risk; Sr and Pu are more likely to be fixed in bones, teeth or liver, thus affecting surrounding tissues for the life of the animal. (iii) Direct or external exposure is of most relevance for γ radiation emitters (e.g., 133Cs) but of limited relevance for α emitters because α particles cannot penetrate the outer layer of skin. Contact with β emitters can also generate burns or eye damage, but this requires close contact as β particles can travel for only limited distances in the air. Exposure by absorption and external exposure are of importance for plants and fungi.

Dose, rate and bystander effects
In all organisms, intracellular DNA is sensitive to radiation exposure and is easily broken by exposure to low amounts of radiation. A double-strand break is often lethal as it is difficult to repair correctly, often leading to the loss of chromosomal material at cell division and, ultimately, cell death. Incorrectly repaired DNA can lead to mutations and carcinogenesis [61].

Point mutations (i.e. single base-pair substitutions) generally show a linear radiation dose response and are more prevalent at low doses. Intermediate doses are often associated with frame shifts (i.e. single base-pair insertions or deletions), whereas high doses often lead to multiple mutations, which can generate intergenic lesions that result in the loss of multiple genes. Such lesions increase with the square of radiation dose [62].

The rate at which a radiation dose is received also influences mutagenesis. In general, there is a linear relationship between mutation rate and dose rate at low dose rates, and an exponential response at high dose rates. Based on observations of DNA repair-deficient cell cultures, low dose rates enable DNA repair, leading to lower mutation rates. Some intragenic lesions (i.e. deletions) are induced by two-hit events (because DNA strands have to be broken twice) and show dose-rate dependence [62]. Independent multilocus mutations are sometimes generated by the same low-energy track as a consequence of the folding patterns of DNA [62].

Recent studies of cell cultures exposed to highly focused low-dose radiation have shown so-called ‘bystander’ effects, whereby non-target cells next to exposed cells show mutagenic effects. The mechanisms underlying bystander effects appear to be diverse and reflect complex pathways of biochemical signalling among cells [61].

Mutation effects
In Table 1 we list 33 studies that investigated mutations or cytogenetic effects of increased radiation around Chernobyl compared with control areas in a variety of plant and animal species. This list is unlikely to be exhaustive, given that there are likely to be further studies published in Russian, Belarusian or Ukrainian journals (usually only in the Russian language) that are thus relatively inaccessible to western scientists. There is considerable heterogeneity in the results, with 25 of the studies showing an increase in mutations or cytogenetic abnormalities. Several studies showed an increase in mutation rates for some loci, but not for others [18,19]. However, many studies were based on small sample sizes, with a resulting low statistical power being unable to show differences of 25% as being statistically significant. Only four of these studies investigated germine mutations [18–21] and these all found significant increases. Many of these studies were not included in the review by the UN Chernobyl Forum Expert Group [1], implying that the conclusions of this group, that germine mutational effects were weak if at all detectable, were not based on available information.

Fitness consequences of the increases in mutation rates or chromosomal aberrations remain largely unknown. Ellegren et al. [19] reported an association between partial albinism and reduced survival in barn swallows; a subsequent study of standardised differences in phenotype for over 30 different characters of barn swallows between study populations near Chernobyl and in relatively uncontaminated control areas revealed a positive relationship between difference in phenotype and effect of the trait on mating success [22]. Mutations with slightly negative fitness effects could easily be exported out of the contaminated areas via organism migration, with consequences for populations that have not been directly exposed to radiation from the disaster. Furthermore, accumulation of mutations in individuals living in contaminated areas could increase the susceptibility of individuals to adverse environmental conditions, because mutants generally will show low levels of stress resistance, although this remains to be tested experimentally. Although the official UN report provided estimates of human deaths attributable to the Chernobyl incident in the order of 10 000 [1], we consider these estimates to be premature, given the current level of knowledge of mutational impact on humans and other organisms. Therefore, more research is needed.

Ecological consequences of radiation
There has been little research on the ecological consequences of the Chernobyl disaster, despite the fact that studies of the abundance of common species of vertebrates and invertebrates can be done easily and at a low cost.

Life-history effects
Life-history consequences of radiation are expected because life-history traits are generally affected by physiological pathways that, on their own, and in combination, can be affected by mutations or the physiological effects of radiation on antioxidant levels [23]. Studies of the barn swallow have shown significant
Box 2. Medical effects of radiation

Radiation emergency workers at the Chernobyl plant during and immediately following the accident received very high doses of radiation and, in total, 57 died. Subsequent investigations of the medical effects of this radiation suggested increased rates of congenital defects, cancers and cardiovascular disease in exposed humans compared with controls. For example, in contaminated areas near Gomel and Mogilev, Belarus, thyroid cancer arising from inhalation of radioactive dust has increased significantly since 1986, as have congenital defects and spontaneous abortions (Figure 1). This is in contrast to the finding of no increase in frequencies of such conditions in several Western European countries over the same time frame [63].

Several studies have also reported increases in the frequency of the medical effects of radiation in control areas, where humans were not exposed to elevated radiation levels [1] (Figure 1). This raises serious problems of interpretation, with some scientists suggesting that effects of ‘worry’ or improved reporting rather than radiation are the cause of such increases. Alternatively, the transition from communism to free market societies around 1990 caused reductions in income, nutritional condition and medical services for much of the human population, which could also explain these results. Unless the confounding effects of such changes can be controlled statistically, there is little possibility of interpreting available medical records reliably. This situation also makes studies of animal or plant models all the more important, both because of their shorter generation times and the lack of importance of ‘worries’ as a cause of any health effects.

The encouraged resettlement of contaminated zones for agriculture in Belarus is based mainly on predictions that <10,000 people are likely to die of Chernobyl-related cancers. Even the best-case scenarios do not include non-cancer mortality or increased morbidity of any sort. Neither is there any assessment of the human costs associated with medical treatment. Given the unprecedented nature of the Chernobyl disaster, it seems prudent to be sensitive to the possible unpredicted impacts, given that many human diseases have long latency periods (e.g. smoking-related illnesses often only occur following 20–30 years of exposure).

Figure 1. Radiation and human health consequences. (a) Increased frequency of spontaneous abortion (red bars, ×0.1) and congenital malformation (white bars) in Gomel and Mogilev, Belarus before and after the Chernobyl disaster. Mean values are shown (s.d.). (b) Increased frequency (per 10,000 inhabitants) of thyroid cancer in children in relation to radiation levels in Belarus (circles) and Ukraine (squares) before and after the Chernobyl disaster, showing an increase after the disaster. Adapted with permission from [1,64].

relationships between background level of radiation and the timing of reproduction, clutch size and hatching success [24]. Non-breeding females are generally uncommon in temperate-zone passerines, but 23% of female barn swallows from Chernobyl were non-breeders and lacked a naked brood patch during the breeding season (breeding female birds moult feathers on their belly to facilitate incubation of eggs), whereas this fraction was close to zero in the control area in Ukraine [24]. The fraction of non-breeders was negatively related to level of background radiation at different sites [24]. Although breeding date has a strong impact on the probability of recruitment in birds [25], there was no delay in breeding associated with an increase in background radiation of two orders of magnitude [24]. The clutch size of barn swallows was reduced in sites with elevated radiation, and hatching failure was associated with background radiation level in this species [24].

Adult survival prospect is an important determinant of life-time reproductive success [26] and any reduction in survival rate will have important fitness consequences. Adult barn swallows breeding in Chernobyl had survival rates that were reduced by 24% and 57% for males and females respectively, in comparison with control areas [24]. These differences are large compared with normal intraspecific variation in survival rate.

Reduced adult survival and reproduction suggests that extant populations of these bird species in this area are unlikely to be viable; only if there is significant immigration from source populations to the Chernobyl sink can these populations be maintained. Based on our current knowledge of source–sink dynamics [27] and known sex differences in adult survival rate and dispersal rate in the barn swallow, we can predict that the rate of immigration should be considerably greater into Chernobyl than into control areas, but only after 1986. Migratory birds winter in specific areas where they tend to return to in subsequent years, and the geochemical fingerprint of these wintering grounds is stored in the stable isotope composition of feathers for those species that moult during winter [28]. This fact was used to investigate the extent to which variance in stable isotope profile differed between barn swallows from Chernobyl and control areas before (using museum material; Box 3) and after the disaster [29]. Stable isotope profiles from before and after the Chernobyl disaster were more heterogeneous than were those of the control population from control areas. Variances in stable carbon isotope content of feathers (δ13C) of both sexes from post-1986 samples from Chernobyl were significantly larger than variances for feather samples from the control region, and compared with variances for historical samples from both regions. This suggests that stable isotope measurements provide information about population processes following environmental perturbations. It also suggests that optimistic prospects for the future of animal and plant populations reported by the UN Chernobyl Forum [1] are biased because apparently healthy populations might be sink populations rather than sources exporting individuals elsewhere.

We can only speculate about the underlying mechanisms that cause the effects of radiation on life history. One possibility is that the reduction in body antioxidant levels directly affects the timing of reproduction, clutch size and survival prospects because female reproduction is limited by antioxidant availability [30]. Similarly, a reduction in antioxidant levels associated with radiation might also have a negative impact on survival prospects, especially in
Box 3. Problems of analyzing effects when there is only one event

The Chernobyl disaster provides an unrivalled opportunity to test the effects of radiation on biological phenomena under large-scale field conditions, given that it is not straightforward to extrapolate from the laboratory to the field. However, this also raises philosophical considerations about how to use a single observation to make rigorous tests of scientific hypotheses. We can imagine three different solutions to this problem, of which two have been adopted so far.

First, investigations that simultaneously use temporal and spatial patterns of a phenomenon can compare the situation before and after the disaster. Such an approach has been used to study partial albinism and asymmetry in feathers of the barn swallow Hirundo rustica before and after the Chernobyl disaster (Figure I; [65]). Partial albinism is caused by mutations that are rare among animals, but the frequency in swallows has increased in the Chernobyl region by five-tenfold since 1986, but not in control areas (Figure I). Similarly, the degree of asymmetry in the length of outermost tail feathers of barn swallows has increased fivefold in Chernobyl, but not in control areas [65]. For many species, comparisons of samples before and after the disaster will not be feasible because of the lack of material pre-dating the disaster.

Second, whereas a given pattern might arise for random reasons with a sample of two, a pattern that occurs repeatedly is unlikely to arise by chance. This approach was used for studies of bilateral asymmetry (e.g. differences in perfect symmetry between the length of right and left characters, such as right and left sides of leaves and right and left wings) in plants and animals in radioactively contaminated areas near Chernobyl and in control areas for a total of 15 species (four plants, four insects, two fish, one amphibian, one bird and three mammals [66–68]). All revealed higher frequencies of asymmetry in representatives from Chernobyl, deviating significantly from the binomial null expectation [69]. However, this method requires many studies of different species.

Third, the heterogeneous spatial distribution of radiation implies that it is unlikely that a similar spatial distribution of phenotype will occur by chance. Thus, an analysis of spatial autocorrelation or a Mantel test is unlikely to provide a significant relationship between radiation and phenotype unless there is an effect of radiation on the phenotypic trait in question, especially if geographical distance is controlled statistically. This approach has yet to be used, although it will provide a useful alternative to previously used methods.

Figure I. Partial albinism in barn swallows. (a) Barn swallows Hirundo rustica with (ai) and without (aii) partial albinism. (b) Frequency of partial albinism in barn swallows Hirundo rustica in Chernobyl (red bars) and control areas (white bars) before and after the disaster. Adapted with permission from [70].

migratory birds that, during the annual migration, produce large amounts of free radicals that must be eliminated to avoid damage to DNA and other molecules [10].

Future prospects for Chernobyl research

Chernobyl constitutes the most extensive ‘natural’ field laboratory for studies of effects of radiation and research during the past 20 years has revealed important insights into the consequences of low- and high-level radiation. However, this ‘facility’ has yet to be fully exploited. It is surprising that there are only a few studies of mutation rates in a small number of species, and that the ecological and evolutionary consequences of low-level radiation remain poorly known. No study has, to our knowledge, investigated whether the disaster has had any effects on population densities of common plants or animals. Likewise, no study has, to our knowledge, attempted to determine whether slightly deleterious mutations arising from Chernobyl are migrating out of the contaminated zone.

This lack of progress is likely to be a result of the low level of investment in research at Chernobyl. Consider the 11 September 2001 event in New York, which resulted in > US$100 billion in funding for all kinds of research, including military research. By contrast, the Chernobyl disaster has attracted < US$10 million over the past 20 years. This lack of funding is far from what one might expect given the non-negligible threat of a ‘dirty’ bomb, the use of nuclear weapons and possible further accidents at nuclear power plants. Even the nuclear power industry and the over-seeing government agencies should have a strong interest in large-scale research to determine the effects of radiation exposure.

We believe that a concerted research effort, funded by the EU, USA, Japan and, to a lesser extent, local
governments, is needed. Such an effort could coordinate research, establish a modern research facility and boost local scientific competence. A major international institute of radiation research supported by the international community would make the most out of one of the largest man-made environmental disasters, to the benefit of the local community, the general scientific community and the world at large.

Table 1. Studies investigating the effects of radiation in Chernobyl on cytogenetics, genetic variability and mutations

<table>
<thead>
<tr>
<th>Species</th>
<th>Genetic marker</th>
<th>Effect</th>
<th>Comments</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Chromosome aberrations</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Human Homo sapiens</td>
<td>Lymphocytes with chromosomal aberrations</td>
<td>Increased by a factor 2–10</td>
<td>In women from Gomel and Mogilev, Belarus</td>
<td>[32]</td>
</tr>
<tr>
<td>Yellow-necked mouse Apodemus flavicollis</td>
<td>Chromosomal aberrations</td>
<td>Increased by a factor 10–20</td>
<td></td>
<td>[33]</td>
</tr>
<tr>
<td>Mouse Mus musculus</td>
<td>Number of reciprocal translocations</td>
<td>Increased by a factor 3–7</td>
<td>In children from Belarus</td>
<td>[33]</td>
</tr>
<tr>
<td>Channel catfish Ictalurus punctatus, Crucian carp Carassius carassius, carp Cyprinus carpio, tench Tinca tinca</td>
<td>Frequency of aneuploidy</td>
<td>Increased aneuploidy in contaminated areas</td>
<td></td>
<td>[36]</td>
</tr>
<tr>
<td><strong>Oligochaetes:</strong> Dero obtuse, Nais pseudobtusa, Nais pardalis</td>
<td>Chromosomal aberrations</td>
<td>Increased by a factor ~ 2</td>
<td>In field populations</td>
<td>[37]</td>
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<tr>
<td>Scots pine Pinus sylvestris</td>
<td>Chromosomal aberrations</td>
<td>Increased by a factor 3</td>
<td>In field populations</td>
<td>[38]</td>
</tr>
<tr>
<td><strong>Somatic mutations</strong></td>
<td></td>
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<td></td>
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<tr>
<td>Human H. sapiens</td>
<td>Minisatellites</td>
<td>Increased rate</td>
<td></td>
<td>[39,40]</td>
</tr>
<tr>
<td></td>
<td>Minisatellites and microsatellites</td>
<td>No significant increase</td>
<td></td>
<td>[41]</td>
</tr>
<tr>
<td></td>
<td>Microsatellites</td>
<td>No significant increase</td>
<td></td>
<td>[42]</td>
</tr>
<tr>
<td></td>
<td>Mutations</td>
<td>No significant increase</td>
<td></td>
<td>[43]</td>
</tr>
<tr>
<td>Bank vole Clethrionomys glareolus</td>
<td>Substitutions in cytochrome b</td>
<td>Multiple substitutions and transversions were restricted to samples from Chernobyl</td>
<td></td>
<td>[45]</td>
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<tr>
<td></td>
<td>Mutations and heteroplasmy</td>
<td>Increased by 19% in mutations and by 5% in heteroplasmy, although not significant</td>
<td></td>
<td>[46]</td>
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<tr>
<td>Mouse M. musculus</td>
<td>Point mutations</td>
<td>No significant increase</td>
<td>Transplant experiment with exposure during 90 days</td>
<td>[47–49]</td>
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<td></td>
<td>Mitochondrial Cytochrome b heteroplasmy</td>
<td>No significant increase</td>
<td>Short-term transplant experiment</td>
<td>[50]</td>
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<td>Channel catfish I. Punctatus</td>
<td>Breakage in DNA</td>
<td>Increased rate of breakage</td>
<td>Changes in DNA content, but unrelated to known measures of contamination</td>
<td>[51]</td>
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<tr>
<td>Crucian carp C. carassius</td>
<td>DNA content based on flow cytometry</td>
<td>Changes in DNA content, but unrelated to known measures of contamination</td>
<td></td>
<td>[52]</td>
</tr>
<tr>
<td>Fruit-fly Drosophila melanogaster</td>
<td>Sex-linked recessive lethal mutations</td>
<td>Increased</td>
<td></td>
<td>[53]</td>
</tr>
<tr>
<td>Wheat Triticum sativum</td>
<td>Microsatellites</td>
<td>Increased by a factor 10</td>
<td>Transplant experiment</td>
<td>[54]</td>
</tr>
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<td>Thale cress Arabidopsis thaliana</td>
<td>Lethal mutations</td>
<td>Increased by a factor 2–4</td>
<td>In greenhouse and field populations</td>
<td>[55]</td>
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<tr>
<td></td>
<td>Lethal mutations</td>
<td>Rate 4-8 times higher than in controls in 1992</td>
<td></td>
<td>[56]</td>
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<td>Scots pine P. sylvestris</td>
<td>Mutation rate at enzyme loci</td>
<td>Increased by a factor 20</td>
<td>In field populations</td>
<td>[55]</td>
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<tr>
<td></td>
<td>Protein-coding genes</td>
<td>Increased by a factor 4–17</td>
<td>In field populations</td>
<td>[55]</td>
</tr>
<tr>
<td><strong>Germline mutations</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Human H. sapiens</td>
<td>Minisatellites</td>
<td>Increased</td>
<td></td>
<td>[18]</td>
</tr>
<tr>
<td></td>
<td>Increased by a factor 1.6 in men only</td>
<td></td>
<td>[21]</td>
<td></td>
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<tr>
<td>Barn swallow Hirundo rustica</td>
<td>RAPDs</td>
<td>Increased rate</td>
<td></td>
<td>[20,57]</td>
</tr>
<tr>
<td></td>
<td>Microsatellites</td>
<td>Increased by a factor 2–10</td>
<td>Increased in only two out of three microsatellites</td>
<td>[19]</td>
</tr>
<tr>
<td><strong>Other effects</strong></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Mouse M. musculus</td>
<td>Lethality, embryo mortality and sterility</td>
<td>Increased</td>
<td>Outcomes of mated laboratory animals</td>
<td>[58]</td>
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<tr>
<td>Wheat T. sativum, rye Secale cereale</td>
<td>Aberrant cells</td>
<td>Increased in a dose-dependent manner</td>
<td></td>
<td>[59]</td>
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</table>
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