Chapter 49
Biological Indicators of Ionizing Radiation in Nature

Anders Pape Møller and Timothy Alexander Mousseau

Abstract Ionizing radiation that consists of α, β and γ rays can directly damage DNA and other molecules and as such result in somatic or germline mutations. The consequences of ionizing radiation for living beings cannot be measured with a Geiger counter because it will depend on external dose, internal dose, and the extent of DNA repair. In addition it will depend on the environmental conditions under which living organisms exist. We list environmental indicators of ionizing condition that reveal immediate and long-term consequences ranging from changes in DNA, over damaged cells and organs to altered gene function and development, reduced fecundity and survival, and hence to negative population trends, and altered communities and ecosystems and perturbed ecosystem functioning. We test for consistency in biological indicator ability across spatial and temporal scales relying on long-term field data collected at Chernobyl and Fukushima, and we test for consistency in indicator ability among indicators. Finally, we address the direct and indirect effects of ionizing radiation and we discuss the species or taxa most susceptible to the effects of radiation.

Keywords Biological level of organization • Consistency across indicators • Direct vs. indirect effects of radiation • Environmental indicators • Spatial consistency • Temporal consistency

49.1 Introduction

Radiation is either non-ionizing (radio waves, visible light and heat) or ionizing with sufficient energy to ionize an atom. Ionizing radiation consists of α particles that cannot penetrate paper, β particles that can penetrate paper, but not an aluminium sheet, and γ rays that can penetrate paper, aluminium, and even layers of lead.

A.P. Møller (✉)
Laboratoire d'Ecologie, Systématique et Evolution, CNRS UMR 8079, Université Paris-Sud, Bâtiment 362, 91405 Orsay Cedex, France
e-mail: anders.moller@u-psud.fr

T.A. Mousseau
Department of Biological Sciences, University of South Carolina, Columbia, SC 29208, USA
e-mail: mousseau@sc.edu

R.H. Armon, O. Hänninen (eds.), *Environmental Indicators*,
DOI 10.1007/978-94-017-9499-2_49

Both ionizing and non-ionizing radiation can damage organisms, although only ions produced by ionizing radiation can directly damage DNA and other molecules. Background radiation dose rates on Earth typically vary from 0.01 to 0.10 μSv/h, with the natural level in Chernobyl before the nuclear accident being only 0.01–0.02 μSv/h. However, some radiation hot spots have levels that exceed global mean levels by three orders of magnitude. The negative effects of radiation have been documented since the first studies of radioactivity by Becquerel and Curie, and the mutation effects of radiation were detected almost 90 years ago (Nadson and Philippov 1925). Thus, the negative consequences of ionizing radiation for living beings are a well-established fact. Still, very little is known about the biological effects of radiation on free-living organisms.

Why not just measure radioactivity with a Geiger counter and use these measures for predicting the consequences of radioactivity rather than investigate how living beings respond to radiation? The main reason is that the consequences of ionizing radiation for living beings will depend on a number of factors, including external dose, internal dose (the amount of radiation due to radionuclides that have been ingested or inhaled), and the extent of DNA repair. There are a large number of radiation hotspots around the world where natural levels of radiation have been shown to have negative effects on mutations, immunology, and disease, despite the opportunity for local adaptation to these conditions (Møller 2012).

A second major reason why the consequences of ionizing radiation cannot just be measured with a Geiger counter is that animals and other organisms that live under normal conditions commonly experience less benign environmental conditions than in the lab. They usually do not have ad libitum access to food and essential nutrients, making them experience trade-offs that are rare or non-existent in the lab. Likewise, field populations commonly suffer from predation, parasitism, or other interspecific interactions, while such effects are effectively controlled or eliminated in lab studies. In fact, most humans also live under such constrained conditions, making it unlikely that lab studies of the effects of ionizing radiation under benign environmental conditions will apply to humans. Indeed, lab studies generally indicate benign effects of low dose radiation, whereas field studies often show considerably increased negative effects (Garnier-Laplace et al. 2012).

Radiation accidents are common, making it of significant importance to document their effects on living beings. The number of radiation accidents runs into the hundreds, with 20 belonging to the grave categories on the International Nuclear Event Scale (INES) 4–7 (Lelieveld et al. 2012). Only Chernobyl and Fukushima have so far been designated as INES 7, which represents major accidents, with four Category 7 events, because of the meltdown of three reactors at Fukushima. Despite these events, there is only limited information available on the biological and health consequences of low dose radiation (reviews in Zakharov and Krysanov 1996; Møller and Mousseau 2006; Yablokov et al. 2009).

The objective of this chapter is to assess biological indicators of ionizing radiation under field conditions as a means of determining the extent to which radiation accidents have immediate and long-term consequences for living beings.

49.2 Environmental Indicators of Ionizing Radiation

49.2.1 Identification of Environmental Indicators of Ionizing Radiation

Mutations are changes in the sequence of DNA caused by single or double strand breakage of DNA. DNA repair can restore the original sequences of DNA, most readily single-strand, but even double-strand breakage of DNA can be repaired efficiently (Lehman 2006; von Sonntag 2010). Mutations are either somatic (i.e., occurring in ordinary body cells) or germ-line (i.e., occurring in gametes). Somatic mutations are sometimes the source of genetic diseases including different types of cancer, while germ-line mutations can be transferred to offspring and hence accumulate across generations. Radiation is a powerful mutagen as shown by classical laboratory experiments (Nadson and Philippov 1925; Muller 1954). Even a natural variation in levels of background radiation is a significant cause of mutation (e.g., Forster et al. 2002) and cancer mortality (e.g., Lubin and Boice 1997; Zhang et al. 2012).

Ionizing radiation can damage DNA either directly by causing single or double strand breakage, or indirectly by the production of free radicals that damage DNA, other molecules, and membranes. Indeed, barn swallows *Hirundo rustica* have germ-line mutation rates for neutral microsatellite markers increased by a factor 2–10 (Ellegren et al. 1997). Numerous other studies have shown increases in mutation rates from bacteria (Ragon et al. 2011) to humans (Dubrova et al. 1996), with contaminated areas around Chernobyl having mutation rates that are increased 2–20-fold relative to controls (Møller and Mousseau 2006). The effects of exposure to ionizing radiation may be long lasting due to genomic instability, causing DNA to be particularly susceptible to future environmental perturbations even after one or more generations (Morgan et al. 1996). Germ-line mutations are not readily quantified under field conditions, mainly because it is difficult to sample DNA from both parents and offspring. In addition, mutations may not have fitness consequences if DNA is repaired, or if offspring carrying mutations are spontaneously aborted, thereby preventing transmission to the next generation.

Mutations may result in the production of non-functional or damaged cells, as in sperm, pollen, red blood cells, and leukocytes. A large fraction of sperm cells has abnormal morphology and behavior, preventing them from fertilization. The frequency of such abnormal sperm is known to increase with the level of background radiation (Møller et al. 2005b), and such sperm cells have inferior swimming behavior, which may prevent fertilization (Møller et al. 2008; Bonisoli-Alquati et al. 2011). A similar production of abnormal germ cells occurs in pollen, which likewise have high frequencies of abnormalities that prevent fertilization. Indeed, the frequency of pollen abnormalities increases strongly with background radiation level in many plant species (Kordium and Sidorenko 1997). Somatic cells might likewise be affected by mutations, as shown for DNA damage to red blood cells in birds (Bonisoli-Alquati et al. 2010).

Ionizing radiation has significant negative effects on the normal development of organs, such as the brain and the lens of the eye. Birds at Chernobyl have brains that are on average 5 % smaller than birds in control areas, and there is strong selection against small brains (Møller et al. 2011). Likewise, the frequency of cataracts due to opacities of the lens is common in free-living birds in contaminated areas, but not in control populations (Mousseau and Møller 2013).

Mutations are a cause of altered DNA sequences that may have negative effects on gene function and hence development of normal morphology. Indeed, the frequency and the extent of abnormalities in plants and animals are elevated in Chernobyl as compared to control areas (Møller 1993, 1998; Zakharov and Krysanov 1996; Møller and Mousseau 2001, 2003). Detailed studies of barn swallows have shown high frequencies of abnormalities in populations in contaminated areas as compared to control populations (Møller et al. 2007). Abnormalities are rare under natural conditions because predators differentially eliminate individuals with aberrant phenotypes. Frequencies of aberrations and hard tumors in a diverse array of bird species reached levels that were many times higher than in control areas (Møller et al. 2013a). Similarly high frequencies of abnormalities have recently been reported for butterflies from Fukushima (Hiyama et al. 2012).

If ionizing radiation affects fertility, this may have negative effects on fecundity. Møller et al. (2005a, 2008) reported significantly elevated hatching failure in birds near Chernobyl compared to control populations, possibly due to embryo mortality caused by either damaged sperm and/or eggs, and hatching failure was also reported for butterflies at Fukushima (Hiyama et al. 2012). The main factors determining fecundity is whether an individual survives to the age of first reproduction and the number of subsequent years of reproduction. Detailed lifetime studies of barn swallows revealed annual adult survival rates reduced to 28 % in contaminated areas compared to 40 % in control populations (Møller et al. 2005a). Across 16 species of birds, adult survival rate was reduced by 21 % in contaminated as compared to control areas (Møller et al. 2012), and it was reduced in butterflies in Fukushima (Hiyama et al. 2012).

If fecundity and survival are reduced in contaminated areas, this translates into reduced abundance and species richness because uncommon species disappear due to random elimination of a few individuals. The underlying mechanisms are poorly understood, although individual birds are know to avoid nesting in the most contaminated areas (Møller and Mousseau 2007b), although contaminated areas that are partly empty due to the negative effects of radiation may be replenished through differential immigration (Møller et al. 2006). Surprisingly, the first standardized counts assessing the relationship between abundance and radiation were not conducted until 2007, more than 20 years after the Chernobyl accident. This is all the more surprising given that such research is inexpensive and does not require special equipment or training. We have made censuses of birds and other organisms (i.e., biotic inventories) at more than 1,000 census points in contaminated areas in Ukraine, Belarus, and Japan using standard procedures (Bibby et al. 2005). Indeed, species richness and abundance of birds (Møller and Mousseau 2007a, b, 2009), but also spiders, dragonflies, grasshoppers, bumblebees, butterflies, amphibians, reptiles, birds, and mammals, are reduced in more contaminated areas in Chernobyl (Møller and Mousseau 2007a, b, 2009, 2011b, 2013) and Fukushima (Hiyama et al. 2012; Møller et al. 2012, 2013b). We have controlled for the potentially confounding effects of habitat, soil, weather, and time of day, but still found highly consistent results (Møller and Mousseau 2011b).

Species and higher taxa differ in their susceptibility to radiation (Møller and Mousseau 2011; Galván et al. 2011). Bird species that have long dispersal and migration distances, pheo-melanin and carotenoid-based plumage, and high fecundity are the most strongly negatively affected by radiation, apparently due to the effects of radiation on the production of free radicals and hence on depletion of antioxidants. Interspecific interactions between species may be affected by radiation if one of the interacting parties is particularly susceptible to radiation. For example, plant-pollinator and prey–predator interactions are affected by radiation if the abundance of pollinators or predators changes. Indeed, mammalian prey were strongly aggregated in the least contaminated sites around Chernobyl, and predators were disproportionately common in those sites, presumably resulting in over-exploitation of prey (Møller and Mousseau 2013).

The effects of ionizing radiation on the abundance and diversity of species may affect interspecific interactions that constitute an integral part of ecosystem functioning. Chernobyl and other areas affected by radiation have perturbed ecosystems (Møller et al. 2012). Radiation reduces the abundance of pollinating insects, such as bumblebees and butterflies, with subsequent negative effects on fruit set of apples, pears, and other fruit bearing plants. In turn, frugivorous birds are less abundant in such areas with few fruit, which negatively affects seed dispersal and hence recruitment. Indeed, the recruitment rate of apples and pears was severely reduced in study plots with elevated background radiation.

49.2.2 Testing for Consistency of Indicator Ability Across Spatial Scales

Large-scale radiation accidents affect hundreds if not thousands of square-kilometers. Still, there have been few attempts to test whether there is consistency in responses to radiation across spatial scales. Møller and Mousseau (2011b) compared breeding bird census data obtained from the same years in Ukraine and Belarus and found highly consistent effects of radiation on the abundance of birds.

We have taken this analysis one step further by analyzing the slope of abundance of different taxa of animals in relation to radiation at Chernobyl and Fukushima (Møller and Mousseau 2013; Fig. 49.1). There was no significant interaction between radiation and area for species richness of birds, number of birds, and number of bumblebees, implying that the effect of radiation was similar in the two areas. In contrast, there were significant interactions for butterflies, dragonflies,

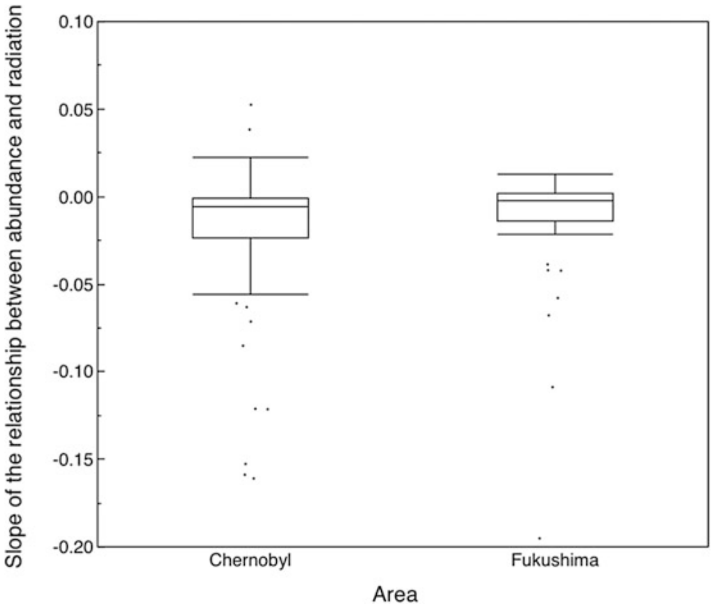

Fig. 49.1 *Box plots* of the slope of the relationship between abundance and level of background radiation for 80 species of birds at Chernobyl and 56 species of birds at Fukushima. The *box plots* show the median, quartiles, 5- and 95-percentiles, and extreme values. Note that slopes were generally negative, implying reduced population sizes at higher radiation levels, and slopes at Chernobyl were more negative than at Fukushima

grasshoppers, and spider webs, implying different effects in the two areas. We should not necessarily expect similarity because Chernobyl has been subject to chronic radiation for 27 years, whereas Fukushima has been exposed only for 2 years, and thus the composition of radionuclides differs.

Interestingly, many species occur both at Chernobyl and Fukushima, allowing a test of similarity in the effect of radiation on abundance at the two sites (Møller et al. 2012). The relationship between abundance and radiation in birds was on average −0.063 (SE = 0.007), N = 80 species in Chernobyl and −0.040 (0.008), N = 45 species in Fukushima. However, among the 14 species occurring at both sites there was a significant interaction between radiation, area, and species, implying that the abundance varied among areas and species, with radiation having different effects. The slope of the relationship between abundance and radiation for the 14 common species was −0.008 (0.001) at Chernobyl, but at −0.067 (0.011) much stronger at Fukushima (Møller et al. 2012).

49.2.3 Testing for Consistency of Indicator Ability over Time

We have conducted censuses of animals at both Chernobyl and Fukushima for more than 1 year, allowing for tests of relationships between abundance and radiation

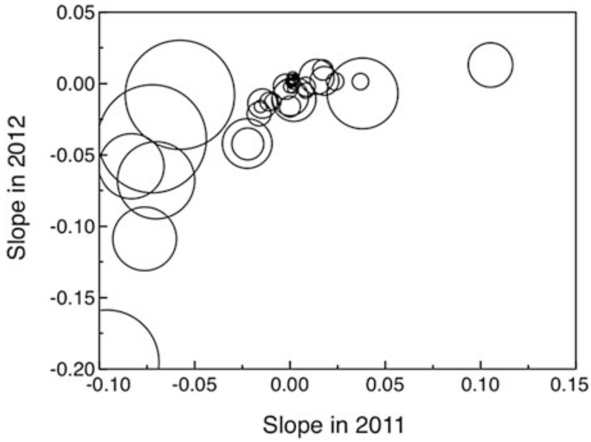

Fig. 49.2 Slope of the relationship between abundance and level of background radiation in 2012 in relation to 2011 for 35 species of breeding birds near Fukushima. The size of the *circles* reflects sample size. The slopes were generally more negative in 2012 than in 2011

among years. Indeed, we have documented temporal consistency for different taxa at Chernobyl and Fukushima (Møller and Mousseau 2011b; Fig. 49.2).

Laboratory experiments on the effects of radiation on living beings are usually based on acute radiation treatment, while the situation in the wild consists of chronic exposure with an accumulation of mutational effects over time. While such accumulation effects have not been demonstrated in Chernobyl because no or few studies were conducted immediately after the accident, Fukushima allows tests of whether there are increasingly detrimental effects over time. While the slope of the relationship between abundance of birds and radiation was −0.006 (SE = 0.005) for 45 species in 2011, it was −0.015 (SE = 0.005) in 2012 for the same species. Thus, the effects of radiation on abundance became much more severe 1 year later as compared to immediately after the accident. If many individuals with abnormalities die, as suggested by studies at Chernobyl (Ellegren et al. 1997; Møller et al. 2013a), we might expect a slight temporal trend toward fewer abnormalities over time due to radioactive decay. Indeed, Møller et al. (2007) showed that there was a trend toward reduced frequency of abnormalities over time in barn swallows, although this reduction could also be due in part to lower radiation doses in some areas following two decades of radioactive decay.

Exposure to radiation may result in adaptive responses to ionizing radiation if there is genetic variation in the underlying mechanisms (i.e., the mechanism(s) of adaptation are heritable), if there is selection against inefficient mechanisms, and if selection occurs for a sufficient number of generations. Recent studies of plants have suggested that DNA repair and specific proteomic patterns provide evidence of such adaptation (Boubriak et al. 2008; Danchenko et al. 2009; Klubicová et al. 2010). However, these experiments are based only on a single sample from a contaminated area and a second from a control area, providing no proper replication, thereby preventing firm conclusions about the underlying cause.

Table 49.1 Environmental indicators of ionizing radiation and their properties in terms of ease of use, consistency in response over space and time, reliability, and information content

Biological level of organization	Feasibility	Cost effectiveness	Consistency over space and time	Reliability	Informative
Mutations, DNA and other molecules	Relatively easy	High	?	?	Weakly
Germ cells	Easy	High	Yes	Yes	Yes
Organs	Easy	High	Yes	Yes	Yes
Populations	Time consuming	High	Yes	Yes	Yes
Species	Time consuming	High	Yes	Yes	Yes
Interactions among species	Time consuming	Medium	Yes	Yes	Yes
Ecosystems	Time consuming	Low	Yes	Yes	Yes

49.2.4 Testing for Consistency of Indicator Ability Among Indicators

Environmental indicators of the effects of radiation on different levels of biological organization have shown strong effects of chronic exposure at Chernobyl more than 27 years after the accident, and on-going studies at Fukushima show increasingly negative effects of radiation with time. Studies of the effects of ionizing radiation at different organizational levels differ in feasibility, cost effectiveness, consistency over space and time, reliability, and information content (Table 49.1). Thus, studies of mutations are relatively easy to conduct, although there are no studies showing consistency in response over space and time. More ecologically oriented studies focusing on populations, species, interactions among species, and ecosystems are time consuming with low cost effectiveness. However, if we require knowledge concerning the effects of radiation at different organizational levels for the characterization of direct and indirect effects and estimation of risks and injuries to individuals, populations, and ecosystems, we must conduct studies at these different levels.

49.3 General Discussion

We have briefly reviewed the literature on indicators of ionizing radiation at different levels of biological organization from molecules and cells, to individuals, populations, species, multi-species interactions, and ecosystems. There are many parallels between the effects observed in natural animal and plant systems and those documented for humans (review in Serdiuk et al. 2011). We have documented consistency in response to radiation over time and space, implying that our findings are not chance relationships, but rather consistent patterns of a pervasive impact of radiation on living systems. This raises two questions: First, what are the direct versus the indirect effects of radiation? Second, at which organizational level is the impact of radiation most efficiently and readily measured? Concerning the first question, there are so far no assessments of the relative direct effects of radiation and the indirect effects of radiation through food availability and interactions with conspecifics, predators, parasites, or pollinators. Clearly, such an assessment is urgently needed.

The second question concerns which species or taxa are most susceptible to radiation and hence most reliable as biological indicators of the effects of radiation (i.e., the canary in the coal-mine analogy). We have previously demonstrated that animal taxa with large mean population density and long natal dispersal distance are most strongly negatively affected by radiation (Møller and Mousseau 2011a). Rare bird species are more strongly negatively affected by radiation, and rare species are disproportionally found in the least contaminated sites around Chernobyl (Møller and Mousseau 2011b). Common species generally have long dispersal distances and occur at high average background radiation levels (Møller and Mousseau 2011b). This effect of dispersal may interact with mutation rate because species that disperse the farthest have the lowest frequency of mutations making it unlikely that mutations spread to uncontaminated areas through dispersal.

49.4 Future Prospects

It has been predicted that another nuclear accident at the INES 7 scale is likely to occur during the next 50 years in a heavily populated area affecting c. 30 million people (Lelieveld et al. 2012). Hence, there is great urgency to learn from past accidents to mitigate future effects. We consider this chapter to constitute a first necessary step toward the production of a tool kit for the assessment of the consequences of future nuclear accidents. Given the poor level of knowledge of the effects of radiation accidents on wild organisms, it is essential to retrieve information at a number of different scales. It is also essential to involve many different people, including citizen scientists, because knowledgeable citizens are numerous and dedicated.

We would like to emphasize the general lack of replication of most studies of low dose radiation. A second major problem is the general lack of proper experimentation with appropriate levels of replication, thus preventing inferences about causation. This precarious situation is mainly due to poor scientific methodology and a chronic lack of funding for research on the effects of low dose radiation. Construction and maintenance of nuclear power plants is hugely expensive, and allocation of even 0.1 per mille would represent a huge boost to research concerning the consequences of radiation accidents.

References

Bibby CJ, Hill DA, Burgess ND, Mustoe S (2005) Bird census techniques. Academic, London

Bonisoli-Alquati A, Voris A, Mousseau TA, Møller AP, Saino N, Wyatt M (2010) DNA damage in barn swallows (*Hirundo rustica*) from the Chernobyl region detected by use of the Comet assay. Comp Biochem Physiol C 151:271–277

Bonisoli-Alquati A, Møller AP, Rudolfsen G, Saino N, Caprioli M, Ostermiller S, Mousseau TA (2011) The effects of radiation on sperm swimming behavior depend on plasma oxidative status in the barn swallow (Hirundo rustica). J Comp Physiol B 159:105–112

Boubriak II, Grozinsky DM, Polischuk VP, Naumenko VD, Guschcha NP, Micheev AN, McCready SJ, Osborne DJ (2008) Mutation and impairment of DNA repair function in pollen of *Betula verrucosa* and seeds of *Oenothera biennis* from differently radionuclide-contaminated sites of Chernobyl. Ann Bot 101:267–276

Danchenko M, Skultety L, Rashydov NM, Berezhna VV, Mátel L, Salaj T, Pret'ová A, Hajduch M (2009) Proteomic analysis of mature soybean seeds from the Chernobyl area suggests plant adaptation to the contaminated environment. J Proteome Res 8:2915–2922

Dubrova YE, Nesterov VN, Krouchinsky NG, Ostapenko VA, Neumann R, Neil DL, Jeffreys AJ (1996) Human minisatellite mutation rate after the Chernobyl accident. Nature 380:683–686

Ellegren H, Lindgren G, Primmer CR, Møller AP (1997) Fitness loss and germline mutations in barn swallows breeding in Chernobyl. Nature 389:593–596

Forster L, Forster P, Lutz-Bonengel S, Willkomm H, Brinkmann B (2002) Natural radioactivity and human mitochondrial DNA mutations. Proc Natl Acad Sci U S A 99:13950–13954

Galván I, Mousseau TA, Møller AP (2011) Bird population declines due to radiation exposure at Chernobyl are stronger in species with pheomelanin-based colouration. Oecologia 165:827–835

Garnier-Laplace J, Geras'kin S, Della-Vedova C, Beaugelin-Seiller K, Hinton TG, Real A, Oudalova A (2012) Are radiosensitivity data derived from natural field conditions consistent with data from controlled exposures? A case study of Chernobyl wildlife chronically exposed to low dose rates. J Environ Radioact 121:12–21

Hiyama A, Nohara C, Kinjo S, Taira W, Gima S, Tanahara A, Otaki JM (2012) The biological impacts of the Fukushima nuclear accident on the pale grass blue butterfly. Nat Sci Rep 2:570

Klubicová K, Danchenko M, Skultety L, Miernyk JA, Rashydov NM, Berezhna VV, Pret'ová A, Hajduch M (2010) Proteomics analysis of flax grown in Chernobyl area suggests limited effect of contaminated environment on seed proteome. Environ Sci Technol 44:6940–6946

Kordium EL, Sidorenko PG (1997) The results of the cytogenetic monitoring of the species of angiosperm plants growing in the area of the radionuclide contamination after the accident at the Chernobyl Atomic Electric Power Station. Tsitol Genet 31:39–46 (in Russian)

Lehman AR (2006) DNA repair. Elsevier, Amsterdam

Lelieveld J, Kunkel D, Lawrence MG (2012) Global risk of radioactive fallout after major nuclear reactor accidents. Atmos Chem Phys 12:4245–4258

Lubin J, Boice J Jr (1997) Lung cancer risk from residential radon: meta-analysis of eight epidemiologic studies. J Natl Cancer Inst 89:49–57

Møller AP (1993) Morphology and sexual selection in the barn swallow *Hirundo rustica* in Chernobyl, Ukraine. Proc R Soc Lond B Biol Sci 252:51–57

Møller AP (1998) Developmental instability of plants and radiation from Chernobyl. Oikos 81:444–448

Møller AP (2012) The effects of natural variation in background radioactivity on humans, animals and other organisms. Biol Rev 88:226–254

Møller AP, Mousseau TA (2001) Albinism and phenotype of barn swallows *Hirundo rustica* from Chernobyl. Evolution 55:2097–2104

Møller AP, Mousseau TA (2003) Mutation and sexual selection: a test using barn swallows from Chernobyl. Evolution 57:2139–2146

Møller AP, Surai PF, Mousseau TA (2005) Antioxidants, radiation and mutation in barn swallows from Chernobyl. Proc R Soc Lond B 272:247–253

Møller AP, Mousseau TA (2006) Biological consequences of Chernobyl: 20 years after the disaster. Trends Ecol Evol 21:200–207

Møller AP, Mousseau TA (2007a) Determinants of interspecific variation in population declines of birds from exposure to radiation at Chernobyl. J Appl Ecol 44:909–919

Møller AP, Mousseau TA (2007b) Birds prefer to breed in sites with low radioactivity in Chernobyl. Proc R Soc Lond B Biol Sci 274:1443–1448

Møller AP, Mousseau TA, Lynn C, Ostermiller S, Rudolfsen G (2008) Impaired swimming behavior and morphology of sperm from barn swallows Hirundo rustica in Chernobyl. Mutat Res 650:210–216

Møller AP, Mousseau TA (2009) Reduced abundance of raptors in radioactively contaminated areas near Chernobyl. J Ornithol 150:239–246

Møller AP, Mousseau TA (2011a) Efficiency of bio-indicators for low-level radiation under field conditions. Ecol Indic 11:424–430

Møller AP, Mousseau TA (2011b) Conservation consequences of Chernobyl and other nuclear accidents. Biol Conserv 114:2787–2798

Møller AP, Bonisoli-Alquati A, Rudolfsen G, Mousseau TA (2012) Elevated mortality among birds in Chernobyl as judged from skewed age and sex ratios. PLoS One 7(4):e35223

Møller AP, Mousseau TA (2013) Assessing effects of radiation on abundance of mammals and predator-prey interactions in Chernobyl using tracks in the snow. Ecol Indic 26:112–116

Møller AP, Mousseau TA, Milinevsky G, Peklo A, Pysanets E, Szép T (2005a) Condition, reproduction and survival of barn swallows from Chernobyl. J Anim Ecol 74:1102–1111

Møller AP, Surai PF, Mousseau TA (2005b) Antioxidants, radiation and mutation in barn swallows from Chernobyl. Proc R Soc Lond B 272:247–253

Møller AP, Hobson KA, Mousseau TA, Peklo AM (2006) Chernobyl as a population sink for barn swallows: tracking dispersal using stable isotope profiles. Ecol Appl 16:1696–1705

Møller AP, Mousseau TA, de Lope F, Saino N (2007) Elevated frequency of abnormalities in barn swallows from Chernobyl. Biol Lett 3:414–417

Møller AP, Bonisoli-Alquati A, Rudolfsen G, Mousseau TA (2011) Chernobyl birds have smaller brains. PLoS One 6(2):e16862

Møller AP, Bonisoli-Alquati A, Mousseau TA (2013a) High frequency of albinism and tumors in free-living birds at Chernobyl. Mutation Res 757:52–59

Møller AP, Nishiumi I, Suzuki H, Ueda K, Mousseau TA (2013b) Differences in effects of radiation on abundance of animals in Fukushima and Chernobyl. Ecol Indic 14:75–81

Morgan WF, Day JP, Kaplan MI, McGhee EM, Limoli CL (1996) Genomic instability induced by ionizing radiation. Radiat Res 146:247–258

Mousseau TA, Møller AP (2013) Elevated frequencies of cataracts in birds from Chernobyl. PLoS One 8(7):e66939

Muller HJ (1954) The manner of production of mutations by radiation. In: Hollaender A (ed) Radiation biology, vol 1, High energy radiation. McGraw-Hill, New York, pp 475–626

Nadson GA, Philippov GS (1925) Influence des rayons x sur la sexualité et la formation des mutantes chez les champignons inferieurs (Mucorinées). C R Soc Biol Filiales 93:473–474

Ragon M, Restoux G, Moreira D, Møller AP, López-García P (2011) Sunlight-exposed biofilm microbial communities are naturally resistant to Chernobyl ionizing-radiation levels. PLoS One 6(7):e21764

Serdiuk A, Bebeshko V, Bazyka D, Yamashita S (eds) (2011) Health effects of the Chornobyl accident: a quarter of century aftermath. DIA, Kiev

von Sonntag C (2010) Free-radical-induced DNA damage and its repair: a chemical perspective. Springer, Berlin

Yablokov AV, Nesterenko VB, Nesterenko AV (2009) Chernobyl: consequences of the catastrophe for people and nature. New York Academy of Sciences, New York

Zakharov VM, Krysanov EY (eds) (1996) Consequences of the Chernobyl catastrophe: environmental health. Center for Russian Environmental Policy, Moscow

Zhang ZL, Sun J, Dong JY, Tian HL, Xue L, Qin LQ, Tong J (2012) Residential radon and lung cancer risk: an updated meta-analysis of case-control studies. Asian Pac J Cancer Prev 13:2459–2465