Review

Conservation consequences of Chernobyl and other nuclear accidents

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ABSTRACT

The explosion at the Chernobyl nuclear power plant on 26 April 1986 released vast amounts of radioactive material over an area of 200,000 km^2 in eastern and central Europe, affecting all living organisms. The biological impacts including the conservation consequences of this event are still poorly known even 25 years after the disaster. Here we assess the effects of this environmental disaster for conservation by focusing on two connected questions addressing the short-term ecological and the long-term evolutionary consequences: First, we pose the question of whether rare species are more impacted by radiation than common species? Second, what are the conservation consequences of elevated mutation rates due to the mutagenic effects of radionuclides from Chernobyl? Furthermore, we assess the extent to which ecological and evolutionary aspects interact. We censused breeding birds across 731 census points in Ukraine and Belarus during 3 years to assess the relationship between abundance of different species and radiation. Most bird species avoided contaminated sites and individuals were concentrated in relatively uncontaminated sites. While common species were recorded at a wide range of radiation levels, rare species were restricted to the least contaminated sites and to sites with a high biodiversity. Thus, rare species were disproportionately impacted by the accident. Mutation rates of plants and animals have increased by up to a factor 20 due to release of radionuclides from Chernobyl. Given that each slightly deleterious mutation is expected to result in a selective genetic death, and that an average fruitfly under normal conditions may carry as many as 80 mutations, the number of mutations in animals and plants around Chernobyl and hence the number of selective deaths is bound to be much higher. There is empirical evidence for highly elevated mortality rates and dramatically increased rates of reproductive failure in contaminated areas, consistent with the expected high frequency of selective deaths due to mutations. The average slightly deleterious mutation is present for 33–167 generations in Drosophila, so if these estimates are qualitatively similar in other organisms, we can expect that mutants will disperse outside contaminated areas resulting in the spread of mutations well beyond the reach of contamination with radionuclides. Therefore, it should be possible to document the gradual spread of mutations from Chernobyl. We consider that the Chernobyl disaster and other nuclear releases may have significant consequences for population size and population viability of many species due to the large number of selective deaths. These effects remain to be investigated. Finally, comparative analyses of birds revealed that species with high mitochondrial DNA substitution rates had short dispersal distances, suggesting that mutations will spread relatively short distances when they are common, but will spread longer distances in species when they are rare.

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1. Introduction

Chernobyl is singularly the largest environmental disaster ever, affecting millions of people (Møller and Mousseau, 2006; Yablokov et al., 2009). Reported estimates suggest fallout equivalent to that from 100 to 400 atomic bombs of the size dropped on Hiroshima and Nagasaki in 1945, with widespread distribution of contaminants across an area about 200,000 km^2 in eastern and central Europe (Yablokov et al., 2009). Additional cases of radioactive contamination have also been reported from the former Soviet Union, UK, USA and most recently the Fukushima region of Japan. In addition, vast areas of the world were contaminated with radioactive fallout stemming from widespread nuclear bomb testing (e.g. Miller, 2002). Furthermore, nuclear power plants habitually emit radioactive gases and liquids by design to the environment under the assumption that this is quickly diluted and hence has little or no significance for humans or free-living organisms (NRC, 2011). Finally, natural levels of background radiation from radionuclides vary by more than two orders of magnitude across the globe with areas with very high levels of natural radioactivity being present in China, India, Iran, Kenya, Namibia, France, Brazil and many other places (Ghiassi-Nejad et al., 2002). Such radiation may occur as radioactive particles in rock or in the form of gases like radon that then can be trapped inside buildings and increase human exposure to mutagens that cause cancer (e.g. Lubin and Boice, 1997; Hendry et al., 2009). Given that additional nuclear accidents seem inevitable, and that all nuclear facilities emit some level of radioactive effluent, there is good reason to address questions related to the conservation consequences of such leakage of radioactive material into the environment.

The biological consequences of radiation from the Chernobyl catastrophe are poorly known because to date rather limited research has been conducted (Zakharov and Krysanov, 1996; Møller and Mousseau, 2006; Yablokov et al., 2009). The general area affected by fall-out from Chernobyl had a background radiation level of only 0.02–0.04 µSv/h, which is among the lowest in the world (Ramzaev et al., 2006). Thus radiation is bound to disproportionately affect local populations due to lack of local adaptation to radiation. Previous studies at Chernobyl have revealed severely reduced species richness, abundance, and population densities of birds in the most contaminated areas (Møller and Mousseau, 2007a,b). Species richness of birds was reduced by 60%, while abundance was reduced by 70% across the more than four orders of magnitude difference in radiation levels that can be found within the exclusion zone (Møller and Mousseau, 2007a,b). Similar, or even more extreme relationships, have been recorded for bumblebees, butterflies, grasshoppers, dragonflies and spiders (Møller and Mousseau, 2011). Birds can actively avoid contaminated areas as shown for pied flycatchers *Ficedula hypoleuca* and great tits *Parus major* when offered a choice between nest boxes in more or less contaminated areas (Møller and Mousseau, 2007c). This suggests that biodiversity in general may be severely depressed in contaminated areas around Chernobyl, despite the fact that the most recent review of the biological consequences of the Chernobyl disaster suggested that the Chernobyl Exclusion Zone was a well-functioning ecosystem with increasing numbers of rare species (Chernobyl Forum, 2005a,b; UN Chernobyl Forum Expert Group "Environment", 2005). However, we note that this assessment was not based on published, quantitative data, and thus we consider this claim to be unsubstantiated until empirical evidence proves otherwise.

The conservation consequences of radiation from the Chernobyl accident or any other nuclear accident have never been addressed explicitly or implicitly in the literature. Thus, there is no empirical or theoretical basis for making a review of this question. Obviously, this does not imply that there are no conservation implications, only that these have so far not yet been studied. Here we suggest that two complementary effects of radioactive contamination occur, short-term ecological effects of radiation that may affect rare species disproportionately, and long-term evolutionary effects due to accumulation of mutations even beyond the immediate area of contamination. These two effects may also show significant interactions because ecological conditions may have synergistic effects at the evolutionary level. For example, mutations may have relatively greater effects on rare than on common species if selective deaths due to mutation affect rare species disproportionately. Likewise, slightly deleterious mutations may migrate outside the areas that are contaminated with dispersing individuals. If species that suffer from high rates of mutation caused by radiation also have high dispersal propensity, such species will suffer disproportionately from migration of mutations outside the contaminated areas. The converse would be the case if such species had relatively short dispersal distances.

Are rare species disproportionately affected by radiation? Rarity could be due to a lack of suitable habitat, a lack of dispersal ability, or a lack of phenotypic characteristics that allow species to reach high population densities. Habitat generalism is an important feature of the ability of different species to exploit available habitats, with specialists having a narrow niche and generalists a broad niche (e.g. Futuyma and Moreno, 1988; Julliard et al., 2006). Specialists are likely to have smaller population sizes than generalists because they can only successfully exploit a narrow range of habitats. Hence, habitat specialization may constitute an important as-

pect of what makes some species rare. Dispersal may affect local abundance and hence the presence of rare species if rare species are particularly susceptible to the effects of dispersal for maintenance of local populations. Dispersal is a mechanism by which local species diversity can increase due to a greater number of immigrants (e.g. Planty-Tabacchi et al., 1996; Levine and D'Antonio, 1999; Stohlgren et al., 1999; Levine, 2000). Furthermore, long-distance dispersal plays an important role in invasions (Shaw, 1995; Koenig et al., 1996), and some studies have suggested that taxa with longer dispersal distances have larger range sizes (e.g. Edwards and Westoby, 1996; Kelly, 1996). Here we analyzed local patterns of biodiversity in a bird community to investigate effects of dispersal propensity on local species richness and the presence of rare species. Thus we pose the question: What are the effects of radioactive contamination from Chernobyl on species that vary in abundance, from locally rare to very abundant species? Are rare species more impacted? Are species with higher threat status more impacted?

There are species-specific differences in impact of radiation on abundance (Møller and Mousseau, 2007b), historical mutation rates (Møller et al., 2010), and current mutation rates (Baer et al., 2007). There are also interspecific differences in the prevalence of phenotypic abnormalities in birds living in areas around Chernobyl (Møller et al., 2007). Given that historical mutation rates as reflected by mitochondrial DNA substitution rates are positively correlated with the extent of the negative effect of radiation on abundance of different species of birds (Møller et al., 2010), this indicates that particular species are consistently susceptible to the effects of mutagens across evolutionary time scales.

Mutagenic effects of radiation were first identified by Nadson and Philippov (1925) for fungi in the 1920s and developed further by Muller (1950). Thus, we should expect the mutational load to increase in areas contaminated with radioactivity. Indeed estimates of mutation rates from the surroundings of Chernobyl suggest that these are increased by up to a factor twenty compared to estimates from uncontaminated control areas (Ellegren et al., 1997; Møller et al., 2005b; review in Møller and Mousseau, 2006). The germline mutation rate is usually much higher in males than in females, especially in older males due to the larger number of germ-cell divisions. Previous studies of DNA substitutions suggest that the rate of deleterious mutation may be sufficiently high to affect disease frequency in humans, and by inference in other organisms as well (Crow, 1997, 2000). The rate of minor deleterious mutations in *Drosophila* fruitflies is on the order of one mutation per zygote (Mukai, 1964), but a much greater number of genes in vertebrates including humans suggests that these effects will be much greater in the latter taxa (Crow, 1997). The mutational cost in terms of fitness was inferred by Muller (1950) to equal one "genetic death". However, selective deaths usually remove multiple mutations thereby reducing the mutational load (Muller, 1950). The effects of mutational leakage from contaminated to uncontaminated areas around Chernobyl are poorly understood. For example, if species with high mutation rates had low dispersal rates, this could reduce the spread of mutations to uncontaminated areas for such species, while an elevated dispersal rate would have the opposite effect. Thus, the effects of dispersal on migration of mutations will partly determine the extent to which different species are affected by mutations beyond the areas of contamination. We will briefly review the arguments addressing these questions.

Although there is no literature addressing the conservation consequences of radiation from Chernobyl or any other nuclear accident, we believe that an assessment of this question is both timely and needed. We use our own extensive data from Chernobyl collected since 1991 to address these important conservation questions. The objectives of this study were to review the impact of radiation from Chernobyl on conservation by investigating the short-term ecological and the long-term evolutionary effects of the Chernobyl accident. Because there is no literature dealing explicitly or implicitly with this subject, we present original research on the relationship between radioactive contamination and abundance. We do so, first, by testing if rare species are disproportionately affected by contamination from Chernobyl. Second, we review the literature on mutational load due to slightly deleterious mutations from a theoretical point of view. Again, there is no literature addressing this question so we review the genetics literature addressing mutational effects in order to arrive at a qualitative assessment of the potential effects. After having reviewed the relationship between mutational load and selective deaths due to mutations, we make an explicit empirical test of whether the frequency of mutations is related to dispersal propensity because such a relationship will affect the rate at which mutations will travel beyond the immediate area that is contaminated and hence the size of the population that is affected by radiation. Specifically, we test if species that are particularly susceptible to the effects of radiation as reflected by high mitochondrial substitution rates differ in dispersal distance from species with low rates because such differences will affect the rate of spread of slightly deleterious mutations beyond the contaminated areas, but also determine which species will be the most affected by mutational load. Because mutation rates in the male germline generally exceed those in the female germline (Crow, 1997; Bartosch-Härlid et al., 2003), we evaluate the consequence of such sex-bias for mutational load. This sex-biased mutation effect is exacerbated by a sex difference in mortality in contaminated areas with a preponderance of male-biased tertiary sex ratios.

2. Material and methods

2.1. Study sites

APM conducted standard point counts during late May – early June 2006–2008 (a total of 731 counts), with each count lasting 5 min during which all birds seen or heard were recorded and identified to species (Møller, 1983; Bibby et al., 2005; Møller and Mousseau, 2007a, 2009b; Voříšek et al., 2010). Points were located at a distance of at least 75 m intervals within forested areas around Chernobyl (Fig. 1). The point counts were made across a range of radiation levels spanning over four orders of magnitude (Fig. 1; Møller and Mousseau, 2007a, 2009a,b). Information on weather (temperature, precipitation, cloud cover, wind), habitats (cover with herbs, shrub, trees, presence of water, type of soil) and date and time of day were recorded at each census point (review in Møller and Mousseau, 2011).

We used abundance of different species of breeding birds summed across all census points as a measure of total abundance. We considered species that were recorded with 1–5 individuals to be rare, and used the number of such species at each census point as an estimate of rare species. The findings reported here did not rely on this specific threshold value because analyses using an upper threshold from 3 to 10 individuals provided qualitatively similar conclusions (results not shown). Thus we only report results for species recorded with 1–5 individuals.

2.2. Confounding variables

We included the following variables in the models because they have previously been shown to predict effects of radiation on the abundance of birds in the neighborhood of Chernobyl (Møller and Mousseau, 2007b).

Fig. 1. Study sites (blue dots) used for censusing birds in the area around Chernobyl and level of background radiation (darker colors imply higher levels of radiation). Modified from European Union (1998). (For interpretation of the references to colors in this figure legend, the reader is referred to the web version of this paper.)

2.2.1. Plumage coloration

We have previously shown that carotenoid- and pheomelanin-based plumage coloration predicts susceptibility to radiation, apparently because radiation results in depletion of antioxidants, and carotenoids and precursors of pheomelanin play important roles as antioxidants (Møller and Mousseau, 2007b; Galván et al., 2011). We scored the breeding plumage of all species as sexually monochromatic if males and females did not differ in coloration according to information provided by the descriptions in Cramp and Perrins (1977–1994), and otherwise as sexually dichromatic, separately for carotenoid- and pheomelanin- and eumelanin-based coloration. We considered sexually dichromatic colors that were yellow, orange and red to be caused by carotenoids, those with chestnut and brown to be caused by pheomelanin and those with black colors to be caused by eumelanin (see Gray (1996), Tella et al. (2004), Olson and Owens (2005), Møller and Mousseau (2007b) and Galván et al. (2011) for similar criteria).

2.2.2. Migration distance

We have previously shown that migration distance predicts susceptibility to radiation, apparently because free radicals produced by migration and radiation compete for antioxidants (Møller and Mousseau, 2007b). We recorded the northernmost and southernmost breeding and wintering latitude to the nearest 0.1° latitude based on the distribution maps in Cramp and Perrins (1977–1994). Migration distance was the difference in the mean of the two breeding latitudes and the mean of the two wintering latitudes.

2.2.3. Dispersal distance

We have previously shown that dispersal distance predicts susceptibility to radiation, apparently because free radicals produced by dispersal and radiation compete for antioxidants (Møller and Mousseau, 2007b). We estimated maximum dispersal distance as the minimum distance from the mainland to an island with a permanent breeding population, using information in Cramp and Perrins (1977–1994). We achieved this by considering the distance from the mainland (usually the European mainland for species with a Western Palearctic breeding distribution) to all islands closer than the furthest island from the mainland (these islands include among others Azores, Madeira, Canary Islands, Iceland, and the islands in the Mediterranean), including those that do not currently hold permanent populations (Møller and Mousseau, 2007b). Therefore, the estimate of maximum dispersal distance was a minimum estimate because many populations on islands are likely not to have taken the shortest route from the mainland to an island, and because islands may have been colonized directly rather than by using intermediate islands as stepping-stones.

As alternative estimates of dispersal distance we used geometric mean natal and breeding dispersal distances based on recoveries or recaptures of birds ringed in the UK (Paradis et al., 1998). These estimates differ from those reported above by Møller and Mousseau (2007b) because we do not know if the estimates by Paradis et al. accounted for effective dispersal since information on breeding status was missing. Previous studies have shown that geometric natal and breeding dispersal distances provide important information on the ecology of birds even beyond UK (e.g. Paradis et al., 1998; Belliure et al., 2000).

We used a third estimate of dispersal distance based on relative richness of subspecies in relation to the size of the breeding range (Belliure et al., 2000). This estimate assumes that a shorter dispersal distance will result in greater phenotypic differentiation and hence a greater richness of subspecies per unit area of the breeding range (Belliure et al., 2000). To estimate relative richness of subspecies we extracted information on number of subspecies from Cramp and Perrins (1977–1994). We estimated breeding range in the Western Palearctic and total breeding range as the area of the shape bounded by the greatest span of latitude and longitude of each species' breeding range, as published in Cramp and Perrins (1977–1994). To take into account the curvature of the earth (which was assumed to be spherical), this area was estimated by the equation

$$\text{Area} = R^2 \times (\text{Longitude}_1 - \text{Longitude}_2) \times (\sin(\text{Latitude}_1) \\ - \sin(\text{Latitude}_2)),$$

where R is the radius of the earth (6366.2 km) and latitude and longitude are expressed in radians.

In widespread species Old and New World ranges were calculated separately and subsequently summed. The method over-estimates true geographical range, but the error should be random with respect to the variables investigated here. Estimates of area were strongly positively correlated with geographical range size as calculated by counting one-degree grid cells overlain on published distribution maps for a sample of 20 Palearctic and Nearctic bird species ($r = 0.87$, $P < 0.001$), and with range size as reported for a sample of 11 threatened species (Stattersfield and Capper, 2000) ($r = 0.98$, $P < 0.001$, based on log-transformed data).

Thus, the different estimates of dispersal distance may account for different aspects of dispersal.

2.2.4. Egg mass

We have previously shown that egg size predicts susceptibility to radiation, apparently because of competition for antioxidants between egg production and exposure to radiation (Møller and Mousseau, 2007b). We recorded egg mass (g) from Cramp and Perrins (1977–1994). If multiple estimates were provided, we extracted the information from UK because those estimates were generally based on the largest sample sizes.

2.2.5. Habitat generalism

Habitat generalism predicts the ability of different species to exploit habitats, with specialists having a narrow niche and generalists a broad niche, thus being able to live in many different places (e.g. Futuyma and Moreno, 1988; Julliard et al., 2006). We recorded the number of breeding habitats by using the breeding habitat sections in Cramp and Perrins (1977–1994). These authors defined a priori the principal habitat categories in a glossary, and only used these for characterization of habitat use. We counted these habitat categories in the breeding habitat descriptions of each species, and this index was used as a measure of habitat generalism (Belliure et al., 2000). Because our study was made independently of the habitat preferences in Cramp and Perrins (1977–1994), we can be assured that we have not introduced any bias in our classification.

As a second measure of habitat specialization we used the habitat specialization index developed by Julliard et al. (2006), defined as the variance in population density among 18 different habitat classes in a nation-wide survey of breeding birds in France. The index values were retrieved from Clavel (2007).

2.2.6. Body mass

We have previously shown that body size predicts susceptibility to radiation, apparently because production of free radicals and hence use of antioxidants depends on body size (Møller and Mousseau, 2007b). We extracted mean body mass of males and fe-

males during the breeding season from Cramp and Perrins (1977–1994), again generally preferring estimates from the UK due to larger sample sizes. Body mass was estimated as the mean value of the means for males and females.

The entire data set is reported in the Supplementary material in the electronic Apendix 1.

2.3. Mitochondrial DNA substitution rates

Species-specific mtDNA base pair substitution rates were used as reported by Nabholz et al. (2008, 2009). Briefly, complete cytochrome *b* sequences for 1571 bird species were aligned and changes in the third base-pair of amino acid encoding codons were used as a measure of genetic divergence (Nabholz et al., 2009). Such changes in the third base-pair of amino acid encoding codons are most often synonymous with respect to amino acid changes and are thus not usually under selection. The third codon position substitution rate provides a good approximation of synonymous substitution rate for two different reasons. First, the vast majority of the cytochrome *b* divergence is synonymous (the ratio non-synonymous/synonymous divergence is close to 2% (Nabholz et al., 2008; Stanley and Harrison, 1999). Second, all the transition substitutions (A ↔ G and T ↔ C) of the cytochrome *b* third codon position are synonymous and most of the substitutions are transitions (the ratio transition/transversion being typically larger than 15 in the dataset). The 1571 species analyzed by Nabholz et al. (2008, 2009) were reduced to 62 species because information on sperm was only available for this reduced subset of species. Studies have suggested that most mutations that occur through oxidative DNA damage are transitions (Wang et al., 1998; Nabholz et al., 2008).

2.4. Measuring background radiation levels

We measured radiation in the field and cross-validated these measurements with those reported by the Ukrainian Ministry of Emergencies. Once having finished the 5 min census we measured α, β, and γ radiation levels at ground level directly in the field at each point where we censused invertebrates using a hand-held dosimeter (Model: Inspector, SE International, Inc., Summertown, TN, USA). All measurements were made according to the instructions for the dosimeter. We measured levels 2–3 times at each site and averaged the results. We cross-validated our measurements against data from the governmental measurements published by Shestopalov (1996), estimated as the mid-point of the ranges published for that particular site. This analysis revealed a very strong positive relationship (linear regression on log–log transformed data: $F = 1546.49$, d.f. $= 1252$, $r^2 = 0.86$, $P < 0.0001$, slope (SE) = 1.28 (0.10)), suggesting that our field estimates of radiation provided reliable measurements of levels of radiation among sites. The measurements by the Ministry of Emergencies were obtained by repeated standardized measurement of radiation at the ground level in a large number of different localities in Ukraine. Radiation levels vary considerably at very short geographical distances due to heterogeneity in the deposition of radiation after the Chernobyl accident (Fig. 1; Shestopalov, 1996), and our measurements at the census points ranged from 0.01 to 379.70 μSv/h, or more than four orders of magnitude.

2.5. Comparative analyses

Because of common ancestry, comparative analyses based on species-specific data overestimate the number of independent observations, thus increasing the risk of statistical type I errors. In order to identify evolutionary independent comparisons we used the method of independent contrasts (Felsenstein, 1985) as implemented in the Macintosh-based software CAIC, using the

CRUNCH algorithm (Purvis and Rambaut, 1995). To do this we constructed a composite phylogeny of all species in our data base (Fig. 1 in electronic Supplementary material 2), based on Sibley and Ahlquist (1990), and updated with recent phylogenies of a more limited range of taxa (Hackett et al., 2008; Jønsson and Fjeldså, 2006). All branches were assigned the same length, because there is no phylogeny based on a single genetic marker that includes all the species included in this study. This procedure is equivalent to assuming an explicit punctuational model of evolution (Purvis and Rambaut, 1995). In alternative analyses we obtained uneven branch length estimates directly from CAIC under the assumption that the ages of taxa are proportional to the number of taxa they contain. This is equivalent to a gradual model of evolution (Purvis and Rambaut, 1995). This second series of analyses provided similar results, and for brevity we thus only report the results from the punctuational models here. Deleting contrasts with extreme residuals to test the robustness of the conclusions did not change the results (Purvis and Rambaut, 1995). Contrasts were analyzed by forcing regressions through the origin, because the dependent variable is expected not to have changed if there is no change in the independent variable (Harvey and Pagel, 1991).

2.6. Statistical analyses

We used generalized linear models throughout. We used an error distribution as appropriate for the response variables. Total abundance of species across all census points, migration distance, dispersal distance, egg mass, body mass and radiation level were $\log_{10}$-transformed. We included all main effects in maximal models, eliminating terms using F-tests for model selection (Crawley, 2002). The statistical significance of each variable was tested in turn using a backward stepwise procedure. The final model was reached when all variables had a significant effect at $P < 0.05$.

We compared the observed distribution of individuals for different species to the expected random distribution to test if the distribution deviated from what would be expected if individuals were distributed according to availability of sites. We also calculated the mean level of radiation at the 731 census points and compared the observed mean level of radiation with this random expectation.

We tested if the mean level of radiation for the occurrence of different species was independent of total abundance, with the alternative hypothesis that rare species should be disproportionately frequent in areas with low radiation and hence high species richness under the hypotheses reported in Section 1.

We tested if rare species were distributed randomly with respect to local species richness and background radiation level, using the census points as independent observations. In this model, we subtracted the number of rare species from local species richness in order to make the two variables statistically independent.

We developed best-fit statistical models to assess the relationship between abundance (response variable) and carotenoid- and eu- and pheo-melanin-based sexual coloration, migration distance, dispersal distance, egg mass, body mass and background radiation level, using the approach described above.

We estimated effect sizes as a reflection of the strength of relationships, using Pearson product-moment correlation coefficients as our metric. We used the guideline by Cohen (1988) that correlation coefficients of 0.10, 0.30 and 0.50, respectively, explaining 1%, 9% and 25% of the variance, are weak, intermediate and strong effects.

All analyses were made with SAS (2000).

3. Results

We first present results about the short-term ecological effects of radiation on abundance and species richness, followed by a sec-

tion on the long-term evolutionary effects of radiation on mutations and mutation accumulation.

3.1. Are rare species particularly susceptible to radioactive contamination?

We recorded a total of 5101 individual birds belonging to 87 species at 731 census points varying in abundance from 1 to 966 individuals for the chaffinch *Fringilla coelebs*, the most abundant species that occurred at 581 of 731 census points, or 79% of all points. Median level of background radiation at the 731 census points was 0.85 μSv/h, allowing us to test if the observed mean level of radiation at points with occurrence of a given species deviated from the random null expectation of 0.85 μSv/h. The observed mean level of background radiation at census points with occurrence of a given species minus the expected level of 0.85 μSv/h should be distributed binomially with half the species having a positive difference and the other half a negative difference. In fact, 69 species had negative differences, while only 18 had positive differences, a highly significant deviation from the binomial expectation ($G = 31.90$, d.f. = 1, $P < 0.0001$). Thus, most species were on average found at mean radiation levels that were lower than expected from a random distribution. A total of 29 out of 87 species, or 33.3%, deviated significantly from a random distribution across levels of radiation, against the expected 5%; a highly significant difference ($G = 68.94$, d.f. = 1, $P < 0.0001$). Finally, mean level of radiation at points of occurrence for the different species was tested against the expected mean value of 0.85 μSv/h. The mean value for the 87 species was 0.45 μSv/h (SE = 1.121; back-transformed from the logarithmic data), differing significantly from the expected value of 0.85 μSv/h (one-sample t-test, $t = -5.66$, d.f. = 86, $P < 0.0001$).

The total abundance of a species across all census points was significantly positively related to the mean level of radiation at occupied sites (Fig. 2). Thus, globally common species were found at more radioactive sites than globally rare species. The absolute frequency of rare species (with a total abundance of 1–5 individuals across all census points) decreased significantly with level of radiation (Fig. 3A; $F = 9.58$, d.f. = 1729, $r^2 = 0.013$, $P = 0.0020$, slope (SE) = −0.009 (0.003)). The frequency of rare species was not randomly distributed among census points differing in species richness, with more rare species tending to occur at census points with higher species richness (Fig. 3B; $F = 19.32$, d.f. = 1729, $r^2 = 0.026$, $P < 0.0001$, slope (SE) = 0.068 (0.015)). The effects of radiation and species richness on frequency of rare species at census points were statistically independent, with a stronger effect of species richness than radiation (partial effect of radiation: $F = 5.03$, d.f. = 1728, $r^2 = 0.007$, $P = 0.025$, slope (SE) = −0.007 (0.003), effect size = 0.08; partial effect of species richness: $F = 8.41$, d.f. = 1728, $r^2 = 0.011$, $P = 0.0039$, slope (SE) = 0.050 (0.017)), effect size = 0.11. Thus, rare species were more common at low radiation levels.

We have previously shown that species that are less common at the most contaminated sites have carotenoid- and phaeomelanin-based plumage, long distance migration, long-distance dispersal and relatively large eggs for their body size (Møller and Mousseau, 2007b; Galván et al., 2011). Therefore, we modeled the total abundance of bird species in relation to radiation and the previously identified five variables, with a statistical model that explained 41% of the variance (Table 1). There was a significant effect of dispersal distance with species with long dispersal distances being globally more abundant across all sites (Table 1). Unsurprisingly, small-sized species were globally more abundant than large species (Table 1). Finally, species that occurred at higher radiation levels were ones that tended to be generally the most abundant across all sites (Table 1). There were no significant effects of carotenoid- or phaeomelanin-based coloration. An analysis of independent

Fig. 2. Total abundance of 87 species of breeding birds around Chernobyl across all census points in relation to the mean level of radiation (μSv/h) at census points where a species was recorded. The positive relationship implies that rare species occur at the least contaminated areas, whereas abundant species are found in the most contaminated areas.

Table 1
Total abundance of 87 different bird species around Chernobyl in relation to dispersal distance (km), body mass (g) and level of background radiation (μSv/h) in analyses of species-specific values and statistically independent linear contrasts. All variables were log-transformed before analysis. The two models had the statistics $F = 19.15$, d.f. = 3,83, $r^2 = 0.41$, $P < 0.0001$ and $F = 25.98$, d.f. = 2,84, $r^2 = 0.24$, $P < 0.0001$.

Variable	Sum of squares	d.f.	F	P	Slope (SE)
Species					
Dispersal distance	2.455	1	7.31	0.0083	0.298 (0.110)
Body mass	2.070	1	6.16	0.015	−0.259 (0.104)
Radiation	13.780	1	41.03	<0.0001	0.544 (0.085)
Error	27.877	83			
Contrasts					
Dispersal distance	0.483	1	5.11	0.026	0.240 (0.106)
Radiation	3.909	1	41.37	<0.0001	0.539 (0.084)
Error	7.938	84			

retained (Table 1). There were no significant effects of carotenoid- or phaeomelanin-based coloration.

We tested if the effect of radiation on overall abundance across all sites remained after inclusion of habitat generalism as an additional predictor variable. Only the habitat specialization index entered this model, while the number of breeding habitats was not included because it explained hardly any of the variance (Table 2). This model for species-specific data that only included habitat specialization index and radiation level accounted for 44% of the variance (Table 2). The effect of radiation was still the best predictor, accounting for 23% of the variance and hence a large effect, while the effect of habitat specialization accounted for 14% of the variance (Table 2). Both these effects were confirmed in analyses of independent contrasts (Table 2).

3.2. Mutational load and radiation

Mutations are generally slightly deleterious, although rare beneficial mutations do occur (Eyre-Walker and Keightley, 2007). Because mutation rates in the male germline generally exceed those in the female germline because of the larger number of cell divisions, especially in older individuals (Crow, 1997), we evaluate the consequence of such sex-bias for mutational load. Crow (1997) discussed at length the health risks that slightly deleterious mutations pose to human societies. The three main points were that (1) substitution rates are higher in males than in females, especially in

Fig. 3. (A) Frequency of rare species of birds at census points around Chernobyl in relation to background radiation levels (μSv/h). Rare species had a total abundance of 1–5 individuals recorded during 2006–2008. Values are means (SE) for census points. (B) Frequency of rare species of birds at census points around Chernobyl in relation to local species richness at census points. Rare species had a total abundance of 1–5 individuals recorded during 2006–2008. Values are means (SE) for census points.

contrasts revealed significant effects of dispersal distance and radiation on overall abundance, while the effect of body size was not

Table 2
Total abundance of 65 different bird species around Chernobyl in relation to habitat specialization and level of background radiation (μSv/h) in analyses of species-specific values and statistically independent linear contrasts. Radiation level was log-transformed before analysis. The two models had the statistics $F = 24.26$, d.f. = 2,62, $r^2 = 0.44$, $P < 0.0001$ and $F = 25.95$, d.f. = 2,62, $r^2 = 0.30$, $P < 0.0001$.

Variable	Sum of squares	d.f.	F	P	Slope (SE)
Species					
Habitat specialization	2.813	1	9.70	0.0028	−0.939 (0.301)
Radiation	5.327	1	18.36	<0.0001	0.416 (0.010)
Error	17.984	62			
Contrasts					
Habitat specialization	0.562	1	7.81	0.0069	−0.812 (0.290)
Radiation	1.510	1	20.98	<0.0001	0.419 (0.092)
Error	4.463	62			

older individuals, due to a large number of cell divisions in the male germline. (2) The number of mutations per generation exceeds the number of zygotes. (3) The most efficient way in which organisms can cope with a high mutation rate is through quasi-truncation selection (instead of a specific cut-off point the probability of selective elimination increases gradually over the range of number of mutations; Crow and Kimura, 1979) resulting in selective deaths with each eliminating a number of mutated genes. Comparative analyses in birds have shown that species with higher frequencies of extra-pair paternity and later age at first reproduction have higher male to female mutation bias (Bartosch-Härlid et al., 2003). This sex-biased mutation effect is exacerbated by a female-biased mortality in contaminated areas around Chernobyl resulting in a preponderance of male-biased tertiary sex ratios (Møller et al., 2005a). This should result in a relatively fewer males contributing genetically to the next generation with subsequent consequences for the effective population size.

How do we estimate mutation effects from Chernobyl? One way is to rely on mutation estimates and their consequences in humans and *Drosophila*. Eyre-Walker and Keightley (1999) used DNA substitution data for humans since divergence from the chimpanzee *Pan troglodytes* to estimate the number of deleterious mutations per zygote. They found a total of 143 non-synonymous substitutions and 231 neutral mutations, and the difference between these two estimates equals 88 deleterious mutations, which account for 88/231 = 38% of mutations having been eliminated through selection. Using an estimated generation time of 25 years gives 1.6 deleterious mutations per zygote per generation. The estimate of the fraction of deleterious mutations may be too low, the time since chimpanzees and humans diverged is estimated with uncertainty, and mutations outside coding regions were disregarded (Eyre-Walker and Keightley, 1999). In conclusion, Eyre-Walker and Keightley (1999) suggested a deleterious mutation rate of three new mutations per zygote, and similar levels may apply to other vertebrates.

We can use this estimate to assess the effects on genetic deaths caused by the effects of deleterious mutations on the probability of survival and reproduction. If fitness is multiplicative, then the probability of survival and reproduction equals $e^{-2\sum\mu}$, where μ is the mutation rate (Crow, 1997). So if $\mu = 1$, then $e^{-2\sum\mu} = 0.37$, and if $\mu = 3$, then $e^{-2\sum\mu} = 0.05$. With the first estimate of one deleterious mutation per zygote, we end up with the rule of Muller (1950) that each mutation leads to a genetic death. However, if mutation rates increase by up to a factor 20, as reported from Chernobyl (Møller and Mousseau, 2006), then the number of genetic deaths would be prohibitively high. How can we resolve this dilemma? Two mechanisms may resolve this problem. First, truncation selection has a fixed threshold of number of deleterious mutations beyond which all individuals die potentially resulting in elimination of multiple mutations. Crow and Kimura (1979) showed that quasi-truncation selection where the probability of selective elimination

increases gradually with the number of deleterious mutations is almost as efficient as truncation selection, with the efficiency reaching 87% under realistic assumptions about the distribution of mutations. Thus selective deaths simultaneously eliminate a number of mutations rather than just a single deleterious mutation. Second, deleterious mutations may not be distributed randomly across the genome. For example, Forster et al. (2002) showed for mitochondrial DNA in humans in response to natural variation in background radiation that mutations were strongly aggregated. This effect will contribute to simultaneous elimination of deleterious mutations. Likewise, genomic instability reflects the situation where particular parts of the genome are susceptible to breakage across generations, as reported for humans and mice exposed to radiation (Morgan et al., 1996; Dubrova et al., 1998), and such instability will tend to cause aggregation of mutations.

The mean number of generations that a slightly deleterious mutant persists in a population is also of importance because it will affect the probability of the mutant migrating outside the area of contamination, but it will also affect the number of generations during which we might be able to detect viability reduction under field conditions. We can estimate this quantity from the reduced viability of heterozygotes and the mutation rate per zygote. The reduced viability due to minor deleterious mutants has been estimated to 0.12 (Temin, 1966). Crow (1997) reviewed estimates of number of generations that deleterious mutants persisted in *Drosophila* populations as 33–167, with a mean estimate of around 80 generations. Thus, if we assume one deleterious mutation per zygote per generation, this implies that an average fruitfly carries 80 mutations. Therefore, we can expect mutations and their fitness effects due to the initial release of radiation from the Chernobyl nuclear reactor in 1986 to persist for a very long time. For example, humans are still in the first generation after the accident (assuming a generation time of 30 years), suggesting that any full assessment of the effects of mutations must await the next many generations. Given that most of the radioactive Cs, Sr and Pu isotopes are still present due to their long half-lives, we can expect mutational effects and high levels of genetic deaths for a very long time. We can also expect the level of these genetic deaths to be high, although exact estimates will require further information on the magnitude of the component parts of the model.

If dispersal distance was correlated with mutation rate, this could determine which species would suffer the most from migration of mutants outside the most contaminated areas around Chernobyl. We made a preliminary test of this idea by relating geometric mean natal and breeding dispersal distance to mitochondrial DNA substitution rate. The latter is positively related to the effect of radiation from Chernobyl on the abundance of birds (Møller et al., 2010). While there was no significant relationship between substitution rate and natal dispersal distance in a model that also included body mass as a predictor variable ($F = 0.78$, d.f. = 1, 23, $P = 0.39$, slope (SE) = −0.135 (0.154)), the relationship

with breeding dispersal distance was significantly negative (F = 7.75, d.f. = 1, 23, P = 0.011, slope (SE) = −0.344 (0.124)). This finding suggests that mutations are less likely to be spread to uncontaminated areas through dispersal in species that are most susceptible to mitochondrial mutations, while species with few mutations are more likely to suffer from the effects of such mutations beyond the immediate area of contamination.

In a second series of analyses we related mitochondrial DNA substitution rate to subspecies richness, adjusted for breeding range size and body mass. Indeed, mitochondrial substitution rate was significantly larger in species with higher subspecies richness (F = 11.07, d.f. = 1, 149, P = 0.0011, slope (SE) = 0.213 (0.064)), after partialling out the effect of body mass (F = 131.85, d.f. = 1149, P < 0.0001, slope (SE) = −0.322 (0.028)). The effect of breeding range size was not statistically significant (F = 0.72, d.f. = 1, 148, P = 0.61, slope (SE) = −0.023 (0.044)). Therefore, mitochondrial DNA substitution rate increased with decreasing dispersal distance, a conclusion that is consistent with the conclusion from the analyses of geometric natal and breeding dispersal distances reported above.

4. Discussion

The main short-term ecological consequences of radiation from Chernobyl were that most species of birds occurred disproportionately often at low radiation levels. Abundant species occurred both a census points with low and high radiation levels, while rare species were restricted to sites with low radiation levels and high species richness. These effects of radiation on abundance were unaffected by potentially confounding variables such as dispersal distance and habitat specialization. The main long-term evolutionary consequences were that mutation rates have increased by up to a factor 20 due to release of radionuclides from Chernobyl. Each such slightly deleterious mutation is expected to result in a selective genetic death. Because average slightly deleterious mutation is present for 33–167 generations in *Drosophila*, mutants will disperse outside contaminated areas resulting in the spread of mutations well beyond the reach of contamination with radionuclides. The Chernobyl disaster and other nuclear releases may have significant consequences for population size and population viability of many species due to the large number of selective deaths. Because elevated mitochondrial DNA substitution rates occurred in bird species with short dispersal distances, mutations will spread relatively short distances in species where they are common, but longer distances in species with less common mutations.

4.1. Radiation and rarity in birds

The effects of the nuclear disaster at Chernobyl on conservation are poorly understood. Extensive areas covering more than 5000 km^2 in Ukraine and Belarus are now largely abandoned without agricultural activity (although forestry activities are conducted to prevent excessive forest fires). Obviously, this has conservation implications because most organisms do better in the absence of human disturbance. Hence, it would not be surprising if the abundance of animals and other organisms had increased in these areas, were it not for the presence of radioactivity. Some scientists have attempted to brand the Chernobyl Exclusion Zone as a wildlife preserve promoting it as a UN cultural heritage site. Others have released a herd of 35 Przewalski's horses *Equus ferus przewalskii* inside the Exclusion Zone (Zharkikh and Yasynetska, 2008), apparently without considering the risk of contamination of the germline of this exceedingly rare species with unwanted mutational load. However, all taxa investigated so far have shown reduced, sometimes dramatically reduced abundance with increasing level of background radiation (Møller and Mousseau, 2011). Here we have reported the results of extensive analyses of bird census data from Ukraine and Belarus to assess the extent to which rare species differed in their response to radioactive contamination from more abundant species. Generalists that occurred in high abundance were found across a wide range of background radiation levels, while rare species were concentrated in relatively uncontaminated areas. The latter areas were also characterized by high species richness that was an independent predictor of the frequency of rare species. Thus, rare species were predominant in areas with high species richness and low levels of radioactivity. Among these rare species recorded in this study there were no directly threatened or endangered species in the study areas although a significant fraction of the globally threatened aquatic warbler *Acrocephalus paludicola* breeds in Belarus and Northern Ukraine (Cramp and Perrins, 1977–1994).

We have so far only considered the direct effects of radioactive contamination on the abundance of bird species. However, there are good reasons to believe that radioactive contamination has increased the importance of parasites in regulating the size of their host populations (Yablokov et al., 2009). This may act through at least two mechanisms. First, increased mutation rates may provide parasites with a selective advantage in the exploitation of their hosts because such hosts will be unable or less able to defend themselves against novel parasite genotypes, and there is direct evidence that bacteria have increased their mutation rates considerably (Ragon et al., 2011). Second, radionuclides may directly weaken the ability of hosts to defend themselves, as in the case of immune defenses of humans against viral and bacterial parasites (Yablokov et al., 2009), or because plants such as wheat *Triticum aestivum* which suffer from reduced proteinase inhibitors that allow wheat rust *Puccinia graminis* to increase its rate and intensity of attack on wheat plants (Dmitriev et al., 2007).

4.2. Mutation rates and mutational load

Populations of barn swallows *Hirundo rustica* and other bird species in the surroundings of Chernobyl cannot be maintained through local recruitment due to low annual adult survival rates and fecundity (Møller et al., 2005a, 2008). Part of this excess mortality may be caused by mutational effects. Given that populations of barn swallows and other species are still present despite low adult survival rates and fecundity implies that immigrants from nearby populations fill vacancies in contaminated areas. We have already published information based on stable isotope profiles consistent with such source-sink dynamics (Møller et al., 2006).

Mutation rates in a diverse array of organisms from Chernobyl have shown increases by up to a factor of 20 (Møller and Mousseau, 2006). Such large increases in mutation rates will have consequences for mutational load and the number of selective deaths needed to eliminate slightly deleterious mutations (Crow, 1997, 2000). In a now classical paper, Muller (1950) suggested that one genetic death would be expected per slightly deleterious mutation. If mutation rates are increased considerably above the levels recorded in radioactively uncontaminated areas, we should expect a very dramatic increase in the frequency of individuals that did not survive or reproduce to such an extent that it would be impossible to maintain viable populations. Given that significant levels of radioactive contamination covers an area of many thousand square kilometers (European Union, 1998), the size of many of the affected bird populations would be in the millions of individuals. Thus, the number of selective deaths required to eliminate the slightly deleterious alleles would be prohibitively high. There is field evidence suggesting that a very large fraction of females does not reproduce in species that otherwise rarely or never skip reproduction (Møller et al., 2005a). Likewise, as many as 28% of all males

from more than 50 species of birds from contaminated areas have no sperm. Furthermore, adult survival rate of barn swallows from contaminated areas is reduced by half compared to populations from uncontaminated control areas (Møller et al., 2005a). Thus there is field evidence consistent with high mutational loads. We might partly eliminate the problem of a prohibitively high number of genetic deaths by the fact that mutations are aggregated on the chromosomes (Forster et al., 2002), and that multiple mutant alleles are likely to be eliminated simultaneously through quasi-truncation selection (Crow, 1997, 2000). In any case, the total number of selective deaths caused by slightly deleterious alleles arising from the mutagenic effects of radiation from Chernobyl is likely to be considerable. Given that the average mutation is likely to persist in populations for up to a hundred generations before being eliminated (Crow, 1997), mutations may be able to spread across large distances due to dispersal, causing detrimental effects far beyond areas that are actually contaminated. For example, Paradis et al. (1998) reported a mean dispersal distance of 69 species of common birds of 2.7 km, or 270 km following 100 generations. If we only consider the most extreme dispersal distances, these distances will increase more than 10-fold (Paradis et al., 1998), implying that already now such mutants may have migrated to western and southern Europe from the main area of contamination in Ukraine. The extent of these effects remains to be determined. However, at least theoretically we should be able to identify the footprint of this event as mutants travel away from Chernobyl through migration, given that numerous deleterious mutations are likely to enter populations of many kinds of organisms due to the mutagenic effects of radiation from Chernobyl.

There was evidence of significant interactions between dispersal and mutations. Comparative analyses revealed significantly lower dispersal distances in species of birds with high mitochondrial DNA substitution rates. That was the case for breeding dispersal distance and relative subspecies richness that is an indirect estimate of dispersal propensity (Belliure et al., 2000). This association may imply that species with higher mutation rates transport mutations through dispersal over shorter mean distances than species with low mutation rates. However, we note that dispersal is notoriously difficult to estimate because a few extreme dispersers that cover very long distances (Koenig et al., 1996) may transport mutations far away.

4.3. Future repercussions of the Chernobyl disaster

The Chernobyl disaster may have additional repercussions that need to be considered by conservation biologists, and we emphasize two issues: (1) Fire risk and the potential transport of radionuclides outside heavily contaminated areas; and (2) movement of radionuclides, especially trans-uranium elements outside the most contaminated areas with migratory birds and other biological agents.

The location of radionuclides is not stable because many different processes including forest fires and fires initiated by humans in agricultural landscapes result in transport of radionuclides outside the most contaminated areas in Ukraine, Belarus and Russia. During the hot summer 2002 radionuclides from Chernobyl were recorded in Vilnius, Lithuania in a concentration that was hundredfold higher than normal, and in August 2010 the concentration of ^{137}Cs in Obninsk, Kaluga near Moscow increased threefold, and on certain days 24-fold (Yablokov et al., 2011, p. 343). Widespread forest fires occurred in contaminated areas during the exceptionally hot and dry summer of 2010 (Charles, 2010), and they are likely to be repeated in the future due to climate change (Barriopedro et al., 2011). In addition, farmers habitually initiate fires in potato stalks and other crop remains during August–October and dry grass in spring, with thousands of small fires

burning in any fall, increasing concentrations of radionuclides manifold in the top soil (Dancause et al., 2010) and releasing radionuclides into the atmosphere. Several hundred fires were burning in early August 2010 in the contaminated areas in Ukraine, Belarus and Russia, many in contaminated areas, and they are likely to have caused increased levels of ^{137}Cs and trans-uranium elements (TUE) in the air. If major forest fires occur in the future, large amounts of radionuclides stored in wood could be transported by smoke and wind to nearby metropolises such as Kiev and Moscow causing major environmental contamination. Policies that attempt to mitigate the long-term accumulation of firewood and the high risk of forest fires in this area with increasing summer temperatures and drought are urgently needed.

Movement of radionuclides, especially trans-uranium elements, but also cesium and strontium outside the most contaminated areas may endanger populations of free-living organisms and humans in areas that are currently little affected by contamination. Particular interest in TUE is due to the majority of these isotopes being alpha emitters with high radiotoxicity and high probability of cancer development. Most TUE fell near the reactor, but noticeable contamination of soil also took place far from Chernobyl due to atmospheric transport, with sizeable concentrations in South Belarus, Western Ukraine and in the vicinity of the Ukrainian capital Kiev. Significant levels of contamination have appeared in areas outside the Chernobyl Exclusion Zone due to transport during the last 25 years (Ministry of Emergencies of Ukraine and Intelligence Systems GEO, Ltd., 2011), and a major source of transport is migratory birds. The levels of internal exposure of people living in these areas exceeds previous predictions manifold. Agricultural activity increases TUE activity in the air by 50–450 times, thus exceeding the specific activity of TUE in the air in the Chernobyl Exclusion Zone, and TUE activity in the air also increases significantly in years of large forest fires (Konoplya et al., 2007). We consider such transport of TUE to potentially be of general conservation concern due to its effects on mutational loads.

In conclusion, we have provided an extensive review of the short-term ecological consequences of the Chernobyl disaster by analyzing the relationship between rarity and level of background radiation in birds. In addition, we have provided extensive information on the long-term evolutionary consequences from the frequency of mutations, mutational load and the potential cost of the Chernobyl disaster in terms of excess selective deaths. The ecological and evolutionary consequences were linked because bird species with short distance dispersal were those with low mitochondrial mutation rates. We consider these ecological and evolutionary factors to potentially have strongly negative effects on the conservation status of many species of birds and by inference also other organisms.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.08.009.

References

Baer, C.F., Miyamoto, M.M., Denver, D.R., 2007. Mutation rate variation in multicellular eukaryotes: causes and consequences. Nature Reviews in Genetics 8, 619–631.

Barriopedro, D., Fischer, E.M., Luterbacher, J., Trigo, R.M., Garcia-Herrera, R., 2011. The hot summer of 2010: redrawing the temperature record map of Europe. Science 332, 220–224.

Bartosch-Härlid, A., Berlin, S., Smith, N.G.C., Møller, A.P., Ellegren, H., 2003. Life history and the male mutation bias. Evolution 57, 2398–2406.

Belliure, J., Sorci, G., Møller, A.P., Clobert, J., 2000. Dispersal distances predict subspecies richness in birds. Journal of Evolutionary Biology 13, 480–487.

Bibby, C.J., Hill, D.A., Burgess, N.D., Mustoe, S., 2005. Bird Census Techniques. Academic Press, London.

Charles, D., 2010. Russia's forest fires ignite concerns about Chernobyl's legacy. Science 329, 738–739.

Chernobyl Forum, 2005a. Chernobyl's Legacy: Health, Environmental and Socio-economic Impacts. IAEA, WHO, UNDP, New York.

Chernobyl Forum, 2005b. Chernobyl: The True Scale of the Accident. 20 years Later a UN Report Provides Definitive Answers and Ways to Repair Lives. IAEA, WHO, UNDP, New York.

Clavel, J., 2007. Habitat Specialization in Birds. PhD Thesis, Université Paris VI, Paris.

Cohen, J., 1988. Statistical Power Analysis for the Behavioral Sciences, second ed. Lawrence Erlbaum, Hillsdale.

Cramp, S., Perrins, C.M., (Eds.), 1977–1994. The Birds of the Western Palearctic, vols. 1–9. Oxford University Press, Oxford.

Crawley, J.M., 2002. Statistical Computing. An Introduction to Data Analysis using S-plus. Wiley, Chichester.

Crow, J.F., 1997. The high spontaneous mutation rate: is it a health risk? Proceedings of the National Academy of Science of the USA 94, 8380–8386.

Crow, J.F., 2000. The origins, patterns and implications of human spontaneous mutation. Nature Reviews in Genetics 1, 40–47.

Crow, J.F., Kimura, M., 1979. Efficiency of truncation selection. Proceedings of the National Academy of Science of the USA 76, 396–399.

Dancause, K.N., Yevtushok, L., Lapchenko, S., Shumlyansky, I., Shevchenko, G., Wertelecki, W., Garruto, R.M., 2010. Chronic radiation exposure in the Rivne-Polissia region of Ukraine: implications for birth defects. American Journal of Human Biology 22, 667–274.

Dmitriev, A., Krizanowska, M., Guscha, N., Grodzinsky, D., 2007. Effect of Low Dose Chronic Irradiation on Plant Disease Resistance and Fungal Pathogen Virulence. Phytosociocentre, Kiev.

Dubrova, Y.E., Plumb, M., Brown, J., Jeffreys, A.J., 1998. Radiation-induced germline instability at minisatellite loci. International Journal of Radiation Biology 74, 689–696.

Edwards, W., Westoby, M., 1996. Reserve mass and dispersal investment in relation to geographic range of plant species: phylogenetically independent contrasts. Journal of Biogeography 23, 329–338.

Ellegren, H., Lindgren, G., Primmer, C.R., Møller, A.P., 1997. Fitness loss and germline mutations in barn swallows breeding in Chernobyl. Nature 389, 593–596.

European Union, 1998. Atlas of Caesium Deposition on Europe after the Chernobyl Accident. EU Publication EUR 16733, Bruxelles.

Eyre-Walker, A., Keightley, P.D., 1999. High genomic deleterious mutation rates in hominids. Nature 397, 344–347.

Eyre-Walker, A., Keightley, P.D., 2007. The distribution of fitness effects of new mutations. Nature Reviews in Genetics 8, 610–618.

Felsenstein, J., 1985. Phylogenies and the comparative method. American Naturalist 125, 1–15.

Forster, L., Forster, P., Lutz-Bonengel, S., Willkomm, H., Brinkmann, B., 2002. Natural radioactivity and human mitochondrial DNA mutations. Proceedings of the National Academy of Science of the USA 99, 13950–13954.

Futuyma, D.J., Moreno, G., 1988. The evolution of ecological specialisation. Annual Reviews of Ecology and Systematics 19, 207–233.

Galván, I., Mousseau, T.A., Møller, A.P., 2011. Bird population declines due to radiation exposure at Chernobyl are stronger in species with pheomelanin-based colouration. Oecologia 165, 827–835.

Ghiassi-Nejad, M., Mortazavi, S.M.J., Cameron, J.R., Niroomand-rad, A., Karam, P.A., 2002. Very high background radiation areas of Ramsar, Iran: preliminary biological studies. Health Physics 82, 87–93.

Gray, D.A., 1996. Carotenoids and sexual dichromatism in North American passerine birds. American Naturalist 148, 453–480.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.-L., Harshman, J., Huddleton, C.J., Marks, B.D., Miglia, K.J., Moore, W.A., Sheldon, F.H., Steadman, D.W., Witt, C.C., Yuri, T., 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320, 1763–1768.

Harvey, P.H., Pagel, M.D., 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford.

Hendry, J.H., Simon, S.L., Wojcik, A., Sohrabi, M., Burkart, W., Cardis, E., Laurier, D., Tirmarche, M., Hayata, I., 2009. Human exposure to high natural background radiation: what can it teach us about radiation risks? Journal of Radiological Protection 29 (2A), A29–A42.

Jönsson, K.A., Fjeldså, J., 2006. A phylogenetic supertree of oscine passerine birds (Aves: Passeri). Zoologica Scripta 35, 149–186.

Julliard, R., Clavel, J., Devictor, V., Jiguet, F., Couvet, D., 2006. Spatial segregation of specialists and generalists in bird communities. Ecology Letters 9, 1237–1244.

Kelly, C.K., 1996. Identifying plant functional types using floristic data bases: ecological correlates of plant range size. Journal of Vegetation Science 7, 417–424.

Koenig, W.D., Van Vuren, D., Hooge, P.N., 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology and Evolution 11, 514–517.

Konoplya, Ye.F., Kudryashov, V.P., Mironov, V.P., 2007. Radiation and Chernobyl: Transuranic Elements on the Territory of Belarus. Institute of Radiology, Gomel.

Levine, J.M., 2000. Species diversity and biological invasions: Relating local process to community pattern. Science 288, 852–854.

Levine, J.M., D'Antonio, C.M., 1999. Elton revisited: a review of evidence linking diversity and invisibility. Oikos 87, 15–26.

Lubin, J., Boice Jr., J., 1997. Lung cancer risk from residential radon: meta-analysis of eight epidemiologic studies. Journal of the National Cancer Institute 89, 49–57.

Miller, R.L., 2002. US Atlas of Nuclear Fallout, 1951–1970. Abridged General Reader Edition, vol. 1. Two-Sixty Press.

Ministry of Emergencies of Ukraine and Intelligence Systems GEO, Ltd., 2011. Atlas Ukraien Radioactive Contamination. Ministry of Emergencies of Ukraine and Intelligence Systems GEO, Ltd., Kiev.

Møller, A.P., 1983. Methods for Monitoring Bird Populations in the Nordic Countries. Nordic Council of Ministers, Oslo.

Møller, A.P., Mousseau, T.A., 2006. Biological consequences of Chernobyl: 20 years after the disaster. Trends in Ecology and Evolution 21, 200–207.

Møller, A.P., Mousseau, T.A., 2007a. Species richness and abundance of birds in relation to radiation at Chernobyl. Biology Letters 3, 483–486.

Møller, A.P., Mousseau, T.A., 2007b. Determinants of interspecific variation in population declines of birds from exposure to radiation at Chernobyl. Journal of Applied Ecology 44, 909–919.

Møller, A.P., Mousseau, T.A., 2007c. Birds prefer to breed in sites with low radioactivity in Chernobyl. Proceedings of the Royal Society of London B 274, 1443–1448.

Møller, A.P., Mousseau, T.A., 2009a. Abundance of insects and spiders in relation to radiation at Chernobyl. Biology Letters 5, 356–359.

Møller, A.P., Mousseau, T.A., 2009b. Reduced abundance of raptors in radioactively contaminated areas near Chernobyl. Journal of Ornithology 150, 239–246.

Møller, A.P., Mousseau, T.A., 2011. Efficiency of bio-indicators for low-level radiation under field conditions. Ecological Indicators 11, 424–430.

Møller, A.P., Mousseau, T.A., Milinevsky, G., Peklo, A., Pysanets, E., Szép, T., 2005a. Condition, reproduction and survival of barn swallows from Chernobyl. Journal of Animal Ecology 74, 1102–1111.

Møller, A.P., Surai, P.F., Mousseau, T.A., 2005b. Antioxidants, radiation and mutation in barn swallows from Chernobyl. Proceedings of the Royal Society of London B 272, 247–253.

Møller, A.P., Hobson, K.A., Mousseau, T.A., Peklo, A.M., 2006. Chernobyl as a population sink for barn swallows: tracking dispersal using stable isotope profiles. Ecological Applications 16, 1696–1705.

Møller, A.P., Mousseau, T.A., de Lope, F., Saino, N., 2007. Elevated frequency of abnormalities in barn swallows from Chernobyl. Biology Letters 3, 414–417.

Møller, A.P., Karadas, F., Mousseau, T.A., 2008. Antioxidants in eggs of great tits *Parus major* from Chernobyl and hatching success. Journal of Comparative Physiology B 178, 735–743.

Møller, A.P., Erritzøe, J., Karadas, F., Mousseau, T.A., 2010. Historical mutation rates predict susceptibility to radiation in Chernobyl birds. Journal of Evolutionary Biology 23, 2132–2142.

Morgan, W.F., Day, J.P., Kaplan, M.I., McGhee, E.M., Limoli, C.L., 1996. Genomic instability induced by ionizing radiation. Radiation Research 146, 247–258.

Mukai, T., 1964. The genetic structure of natural populations of *Drosophila melanogaster*. 1. Spontaneous mutation rate of polygenes controlling viability. Genetics 50, 1–19.

Muller, H.J., 1950. Our load of mutations. American Journal of Human Genetics 2, 111–176.

Nabholz, B., Glemin, S., Galtier, N., 2008. Strong variations of mitochrondrial mutation rate across mammals: the longevity hypothesis. Molecular Biology and Evolution 25, 120–130.

Nabholz, B., Glemin, S., Galtier, N., 2009. The erratic mitochondrial clock: variations of mutation rate, not population size, affect mtDNA diversity across birds and mammals. BMC Evolutionary Biology 9, 54.

Nadson, G.A., Philippov, G.S., 1925. Influence des rayon's x sur la sexualité et la formation des mutantes chez les champignons inferieurs (Mucorinées). Comptes Rendus de la Societé de la Biologie et de ses Filiales 93, 473–474.

NRC, 2011. Appendix I to Part 50 – Numerical Guides for design objectives and limiting conditions for operation to meet the criterion "As Low as is Reseaonably Achievable" for radioactive material in light-water-cooled nuclear power reactor effluents. In: NRC Regulations, Title 10, Code of Federal Regulations. US Nuclear Regulatory Commission, Washington, DC.

Olson, V., Owens, I.P.F., 2005. Interspecific variation in the use of carotenoid-based coloration in birds: diet, life history and phylogeny. Journal of Evolutionary Biology 18, 1534–1546.

Paradis, E., Baillie, S.R., Sutherland, W.J., Gregory, R.D., 1998. Patterns of natal and breeding dispersal in birds. Journal of Animal Ecology 67, 518–536.

Planty-Tabacchi, A.-M., Tabacchi, E., Naiman, R.J., Deferrari, C., Décamps, H., 1996. Invasibility of species-rich communities in riparian zones. Conservation Biology 10, 598–607.

Purvis, A., Rambaut, A., 1995. Comparative analysis by independent contrasts (CAIC): an Apple-Macintosh application for analyzing comparative data. Computer Applications in the Biosciences 11, 247–251.

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

Ramzaev, V., Yonehara, H., Hille, R., Barkovsky, A., Mishine, A., Sahoo, S.K., Kurotaki, K., Uchiyama, M., 2006. Gamma-dose rates from terrestrial and Chernobyl radionuclides inside and outside settlements in the Bryansk region, Russia in 1996–2003. Journal of Environmental Radioactivity 85, 205–227.

SAS Institute Inc., 2000. JMP. SAS Institute Inc., Cary.

Shaw, M.W., 1995. Simulation of population expansion and spatial pattern when individual dispersal distributions do not decline exponentially with distance. Proceedings of the Royal Society of London B 259, 243–248.

Shestopalov, V.M., 1996. Atlas of Chernobyl Exclusion Zone. Ukrainian Academy of Science, Kiev.

Sibley, C.G., Ahlquist, J.E., 1990. Phylogeny and Classification of Birds. Yale University Press, New Haven.

Stanley, S.E., Harrison, R.G., 1999. Cytochrome b evolution in birds and mammals: an evaluation of the avian constraint hypothesis. Molecular Biology and Evolution 16, 1575–1585.

Stattersfield, A.J., Capper, D.R., 2000. Threatened Birds of the World. Lynx, Barcelona, Spain.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Scheli, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M., Son, Y., 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69, 25–46.

Tella, J.L., Figuerola, J., Negro, J.J., Blanco, G., Rodriguez-Estrella, R., Forero, M.G., Blazquez, M.C., Green, A.J., Hiraldo, F., 2004. Ecological, morphological and phylogenetic correlates of interspecific variation in plasma carotenoid concentration in birds. Journal of Evolutionary Biology 17, 156–164.

Temin, R.G., 1966. Homozygous viability and fertility loads in Drosophila melanogaster. Genetics 53, 27–46.

UN Chernobyl Forum Expert Group "Environment", 2005. Environmental Consequences of the Chernobyl Accident and their Remediation: Twenty years of Experience. IAEA, WHO, UNDP, New York, NY.

Voříšek, P., Klvanova, A., Wotton, S., Gregory, R.D., 2010. A Best Practice Guide for Wild Bird Monitoring Schemes. European Union, Bruxelles.

Wang, D., Kreutzer, D., Essigmann, J., 1998. Mutagenicity and repair of oxidative DNA damage: insights from studies using defined lesions. Mutation Research 400, 99–115.

Yablokov, A.V., Nesterenko, V.B., Nesterenko, A.V., 2009. Chernobyl: Consequences of the Catastrophe for People and Nature. New York Academy of Sciences, New York.

Yablokov, A.V., Nesterenko, V.B., Nesterenko, A.V., Dobrovol'skaya, N., 2011. Chernobyl: Consequences of the Catastrophe for People and Nature. Universarium Publications, Kiev.

Zakharov, V.M., Krysanov, E.Yu. (Eds.), 1996. Consequences of the Chernobyl Catastrophe: Environmental Health. Center for Russian Environmental Policy, Moscow.

Zharkikh, T.L., Yasynetska, N.I., 2008. Demographic parameters of a Przewalski horse (Equus przewalskii Polj., 1881) population in the Exclusion Zone of the Chernobyl Power Plant. Biological Series 113 (5), 3–9.