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Differences in effects of radiation on abundance of animals in Fukushima and Chernobyl

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ABSTRACT

Radioactive contamination can negatively affect the abundance of living beings through the radiation and chemical toxic effects of radionuclides or the effects of mutation accumulation over time. If radiotoxic effects were the main determinant of the abundance of organisms, we should expect a reduction in abundance immediately following radioactive contamination, while we should expect a gradual increase in negative effects over time if mutation accumulation was the main determinant. In particular, we should expect the main effects at the recently contaminated site in Fukushima to mainly be due to radiotoxicity, while effects at Chernobyl which has been contaminated since 1986 should be a mixture of radiotoxic and mutation accumulation effects. We censused spiders, grasshoppers, dragonflies, butterflies, bumblebees, cicadas and birds at 1198 sites in Chernobyl and Fukushima-Daiichi, where major nuclear accidents happened 25 years and 6 months ago, respectively. The mean level of radiation was higher and less variable at Fukushima than at Chernobyl, implying that we should expect more negative effects on the abundance of animals at Fukushima if immediate effects of radiation were important. While all taxa showed significant declines in abundance with increasing level of background radiation in Chernobyl, only three out of seven taxa showed such an effect at Fukushima. The effect of radiation on abundance differed between the two areas for butterflies, dragonflies, grasshoppers and spiders, but not for birds or bumblebees. These findings are consistent with the main effects of radiation on the abundance of animals at Fukushima being due to radiotoxicity while those at Chernobyl may be due to a mixture of radiotoxicity and mutation accumulation, because chronic exposure have been present for many generations thereby allowing for accumulation of mutations.

1. Introduction

In nature radioactive material occurs as a consequence of natural deposition in rocks or as an accidental consequence of human release of radioactive material such as during nuclear testing, normal maintenance of nuclear power plants and nuclear accidents such as those at Chernobyl and Fukushima Daiichi. Natural levels of radiation sometimes exceed low baseline levels in uncontaminated areas by several hundred-fold (Ghiassi-Nejad et al., 2002), resulting in significant rates of disease and associated mortality in humans (e.g. Lubin and Boice, 1997; Hendry et al., 2009) and by inference also in other organisms. Much higher levels of radiation occur as a consequence of radiation accidents that have produced levels that exceed normal background levels by a factor 10,000 or more.

Radiation can have short-term direct radiotoxic effects or long-term indirect mutation effects on living organisms. The short-term radiotoxic effects include oxidative stress (e.g. Ben-Amotz et al., 1998; Møller et al., 2005b; Bonisoli-Alquati et al., 2010a), increased damage to DNA (e.g. Sakharov et al., 1996; Bonisoli-Alquati et al., 2010b), immuno-suppression (e.g. Camplani et al., 1999; Yablokov et al., 2009) and many others. Such physiological effects can result in reproductive failure and death. Reproductive failure associated with radiation occurs as a consequence of embryo mortality (Møller et al., 2005a, 2008; Yablokov et al., 2009). Reproductive failure has also been reported for birds such as barn swallows *Hirundo rustica* in which more than 25% of females living in contaminated areas may forego reproduction altogether (Møller et al., 2005a), and

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similar reduced fecundity has been reported for humans (Yablokov et al., 2009). Males living in contaminated areas have shown a failure to produce sperm, or if producing sperm then mainly inviable sperm (Yablokov et al., 2009). Short-term physiological effects of radiation may have negative consequences for adult survival, especially in the sex that invests the most in reproduction (Møller et al., 2005a; Yablokov et al., 2009).

Mutation effects due to radioactive contamination are widespread, although more difficult to study due to their long-term nature that can extend across generations. Mutations arise from DNA damage that is not repaired thereby causing a reduction in fitness (Eyre-Walker and Keightley, 2007). Radioactive contamination has been known to be mutagenic for almost a century (Nadson and Philippov, 1925). Extensive studies of a diverse array of plants, animals and other organisms have shown increased levels of mutations by a factor 2 to 20 around Chernobyl (review in Møller and Mousseau, 2006), and a recent meta-analysis has shown strong effects of radiation on mutation rates arising from Chernobyl in a study based on 151 estimates from 45 studies of 30 species (S. Randic, unpublished data). A high rate of deleterious mutations can increase the frequency of disease in humans (Crow, 1997, 2000) and therefore also most likely in other organisms. Mutations are costly because each deleterious mutation equals a "genetic death", although selective deaths may simultaneously reduce the mutational load because multiple mutations are lost simultaneously (Muller, 1950). Alternatively, truncation selection or quasi-truncation selection simultaneously eliminate multiple mutations if the probability of death is a direct function of the number of deleterious mutations. Because slightly deleterious mutations may remain in populations for an extended number of generations (in *Drosophila* on average 80 generations), there is a high probability of such mutations being transmitted during their long-term persistence in a population, resulting in mutation accumulation and mutational load, particularly if mutation effects are recessive (Crow, 1997).

The objectives of this study were to test whether differences in the number of generations that have passed since exposure to radioactive contamination have had an influence on the relationship between the abundance of animals and radiation. We used extensive census data on diurnally active animals around Chernobyl and Fukushima to test (1) whether the abundance of animals was more severely depressed in areas with higher levels of radiation (i.e. Fukushima) or (2) whether the reduction in abundance was the greatest in the area that had exposed animals to radiation for a larger number of generations (i.e. Chernobyl). We should expect radiotoxic effects in both sites, while mutations would only accumulate across generations in Chernobyl, where most organisms have been chronically exposed to radiation for many generations.

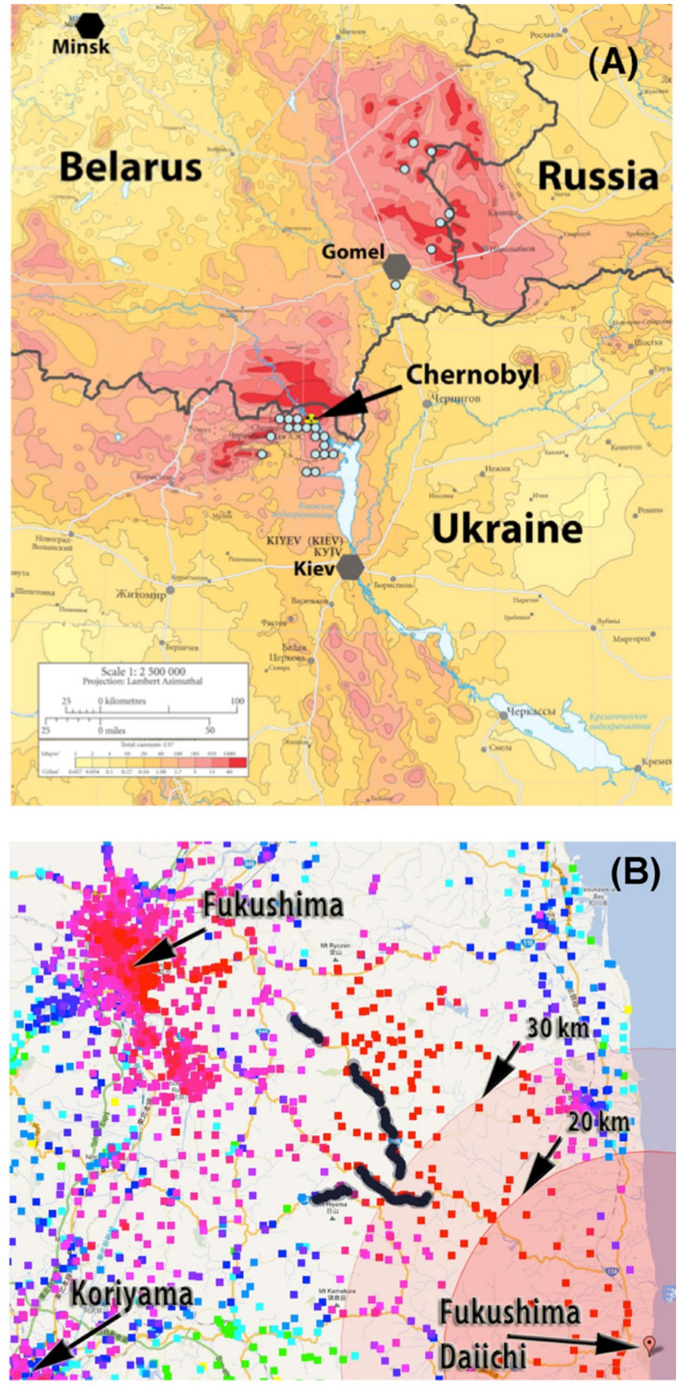

Fig. 1. Location of census areas around (A) Chernobyl, Ukraine and Belarus and (B) Fukushima, Japan. Census points in Fukushima are located in six areas. Note that levels of radiation in Fukushima have only been recorded at a limited number of sites.

Adapted from Shestopalov (1996) and http://www.nnistar.com/gmap/fukushima, a map generated by the Japanese Ministry of Education, Culture, Sports, Science and Technology (MEXT) and local government officials.

2. Methods

2.1. Study sites

The censuses were conducted within the Chernobyl Exclusion Zone or adjacent areas on the southern and western borders with a permit from the Ukrainian authorities and in areas in southern Belarus around Gomel during the breeding seasons 2006–2009 (Fig. 1A). A total of 254 points in 2006, 235 points in 2007, 237 points in 2008 and 159 points in 2009 were located at ca. 100 m intervals within forested areas (excluding successional stages of secondary forest due to abandoned farming (these areas are still almost exclusively open grassland)).

We conducted similar censuses at a total of 300 sampling points in forested areas west of the exclusion zone around the Fukushima Daiichi power plants in 2011 (Fig. 1B). At least one local ornithologist participated in the censuses in Japan to confirm the identity of some difficult bird species. All sampling sites were identified using GPS coordinates.

2.2. Animal censuses

The point count census method provides reliable information on relative abundance of birds (Møller, 1983; Bibby et al., 2005;

Voříšek et al., 2010) and other organisms. It consists of counts lasting 5 min during which the number of spider webs, and the number of individual grasshoppers, dragonflies, bumblebees, butterflies, cicadas, amphibians, reptiles and birds seen or heard were recorded. APM (wearing a radiation protection suit in the most contaminated areas in Chernobyl) conducted these standard point counts during 29 May to 9 June 2006, 1 to 11 June 2007, 29 May to 5 June 2008, 1 to 6 June 2009 in Chernobyl and surroundings and during 11 to 15 July 2011 in Fukushima. The fact that one person made all counts eliminates any variance in results due to inter-observer variability.

We directly tested the reliability of our counts by letting two persons independently perform counts, and the degree of consistency was high for both species richness and abundance (details reported by Møller and Mousseau, 2007a).

Mammal censuses were conducted using 161 line transects each with a length of 100 m along roads in a large number of areas in the Chernobyl exclusion zone and just outside the zone during 3–4 February 2009. Mammals were identified from footprints in fresh snow using a standard field guide (Bang et al., 2007). See Møller and Mousseau (2011) for further details.

2.3. Confounding variables

Abundance estimates can be affected by numerous confounding variables (Voříšek et al., 2010), and, therefore, it is important to control such variables statistically to assess the underlying relationship between radiation and species richness and abundance. We classified habitats (agricultural habitats with grassland or shrub [either currently or previously cultivated], deciduous forest, or coniferous forest) and estimated to the nearest 10% ground coverage by herbs, shrub, trees, agricultural habitat, deciduous forest and coniferous forest within a distance of 50 m from the census points. We recorded altitude to the nearest foot, using a GPS. Weather conditions can affect animal activity and hence census results (Voříšek et al., 2010), and we recorded cloud cover at the start of each point count (to the nearest eighth), temperature (degrees Celsius), and wind force (Beaufort). For each census point we recorded time of day when the count was started (to the nearest minute). Because activity may show a curvilinear relationship with time of day, for example, with high levels of activity in the morning and to a lesser extent in the evening for birds (Voříšek et al., 2010), and higher levels of activity for thermophilic vertebrates and invertebrates, we also included time squared as an explanatory variable.

Møller and Mousseau (2011) have previously used estimates of natal dispersal distance (the distance between the site of emergence/birth to the future site of reproduction (Clobert et al., 2001)) for different taxa to explain the slopes describing the relationship between abundance and level of background radiation. We used their estimates reported in Appendix A in Møller and Mousseau (2011). We estimated mean abundance of different taxa as the mean number of individuals recorded at the census points.

2.4. Background radiation

We measured radiation in the field and cross-validated these measurements with those reported by the Ukrainian Ministry of Emergencies. After having finished the 5 min census we measured radiation levels at ground level directly in the field at each point where were censused invertebrates using a hand-held dosimeter (Model: Inspector, SE International, Inc., Summertown, TN, USA). We measured levels two to three times at each site and averaged the results. We cross-validated our measurements in Ukraine against data from the governmental measurements published by Shestopalov (1996), estimated as the mid-point of the ranges published. 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.

Measurements at Fukushima were obtained using the same dosimeters which were cross-validated with readings with a dosimeter that had been recently calibrated and certified to be accurate by the factory (International Medcom, Sebastopol, CA, USA). We also made a cross-validation test at Fukushima by comparing our own measurements using the Inspector dosimeter with measurements obtained at the same locations with a TCS 171-ALOKA. Again, there was a very strong positive relationship (linear regression on log–log transformed data: $F = 2427.97$, d.f. = 1, 20, $r^2 = 0.99$, $P < 0.0001$, slope (SE) = 1.120 (0.023)).

There were significant differences between Fukushima and Chernobyl in the nature of the disaster as well as the type and the amounts of radionuclides that were released to the environment. Currently, for terrestrial ecosystems, in Fukushima cesium-134 and cesium-137 predominate (Kinoshita et al., 2011), while in Chernobyl cesium-137, strontium-90, various isotopes of plutonium, and americium-241 are found at biologically significant levels across the landscape (Voitsekhovich et al., 2007), and differential sensitivity to these mixtures could account for some of the differences in biological responses observed between sites.

Cesium 137, with a half-live of about 30 years, decays by beta emission primarily to a meta-stable isomer of barium-137, which is responsible for the gamma emissions of this isotope (Baum et al., 2002). Thus if ingested, cesium-137 will generate both beta and gamma doses for living organisms. Cesium-134 that has a half-life of about 2 years is exclusively a beta emitter and is thus mainly a concern if ingested.

Strontium-90, with a half-life of about 29 yrs, is almost a pure beta emitter.

Most isotopes of plutonium are alpha emitters and are thus primarily of concern if ingested. However, plutonium-241, which is present to a significant degree in the Chernobyl region, has a half-life of about 14 yrs, and decays via beta emissions to americium-241 (half life of 432 years), which in turn decays via alpha emissions to neptunium-237, with gamma emissions as an additional by-product.

Although handheld Geiger counters are likely to provide reliable measures of background contamination levels of radionuclides for gamma sources, and to a lesser degree for beta emitters, if the Geiger detector is in close proximity to the source, characterization of alpha emitters usually requires more complex measurement methods that are usually only tractable in a laboratory setting due to the short transmission distance of alpha particles in air.

Given the different characteristics of radionuclides in the environment at Fukushima and Chernobyl, field measurements of contaminant levels are likely to underestimate biologically relevant radiation levels in Chernobyl when the main exposure pathway is via ingestion. Similarly, background radiation measures in the areas of Chernobyl closest to the reactor (e.g. the Red Forest) are very likely to underestimate biologically relevant doses given the abundance of alpha emitting actinides (e.g. plutonium isotopes) that were differentially deposited in this area.

2.5. Statistical analyses

We analyzed the levels of radiation at the census points using Welch ANOVA for samples with unequal variance. Normal quantile plots were used to illustrate the spatial distribution of radiation.

Radiation level and abundance were $\log_{10}$-transformed, while ground coverage with farmland, deciduous and coniferous forest, grass, bush and trees was square root arcsine-transformed. We included these variables in addition to temperature, cloud cover, wind, time of day and time of day squared. We also included radiation level squared to account for non-linear relationships between species richness and abundance, respectively, and radiation. We developed statistical models to assess the relationship between abundance (response variables) and radiation, assuming a Poisson distribution of abundance, after inclusion of the potentially confounding variables, as implemented in the statistical software JMP (SAS Institute Inc., 2000).

We quantified the relationship between abundance of different taxa and level of radiation by estimating the slope of the relationship between abundance and $\log_{10}$-transformed radiation. These slopes were used for subsequent analyses. We tested whether mean slopes differed from zero using a one-sample *t*-test. Finally, we tested if slopes for different taxa could be explained by estimates of natal dispersal distance (derived from Møller and Mousseau, 2011) and mean population density at census points.

3. Results

3.1. Radiation levels

Radiation levels at the census points at Fukushima ranged from 0.55 to 30.76 μSv/h, mean (SD) 5.15 μSv/h (3.05), $N = 300$ census points, and from 0.01 to 379.70 μSv/h, mean (SD) 0.88 μSv/h (13.50), $N = 898$ census points at Chernobyl, following back-transformation of the log-transformed values. The frequency distribution of radiation levels at census points in Chernobyl was much more skewed than that from Fukushima, with many census points with low levels and a few having very high levels (Fig. 2). The mean values at census points were significantly higher at Fukushima (Welch ANOVA $F = 265.92$, d.f. = 1, 1129.3, $P < 0.0001$), while the variance at census points was larger at Chernobyl (Levene's test: $F = 199.16$, d.f. = 1, 1196, $P < 0.0001$).

3.2. Abundance of animals and level of radiation

The abundance of birds, butterflies and cicadas decreased significantly with level of background radiation at Fukushima, while that was not the case for bumblebees, dragonflies and grasshoppers (Table 1). Spiders were the only taxon that increased in abundance with increasing level of radiation (Table 1). The abundance of all investigated taxa decreased with level of background radiation at Chernobyl (Table 1). The mean of the slopes describing the relationship between abundance and level of background radiation for different taxa was statistically significant for Chernobyl (mean (SE) = −0.059 (0.015), $N = 10$ taxa, $P = 0.0041$), while that was not the case for Fukushima (mean (SE) = −0.040 (0.106), $N = 8$ taxa, $P = 0.32$). Analyses that included all environmental variables provided similar conclusions to those reported in Table 1 (Electronic Supplementary Material Table 1). The slope of the relationship between abundance and radiation for different taxa was strongly positively correlated with the slope after adjusting for potentially confounding environmental variables ($F = 33.98$, d.f. = 1, 6, $r^2 = 0.85$, $P = 0.0011$, slope (SE) = 1.668 (0.286)), and the two sets of slopes differed significantly (paired *t*-test, $t = 2.24$, d.f. = 7, $P = 0.03$).

Census data from Chernobyl and Fukushima were used to test if abundance was related to background radiation, if abundance differed between the two sites, and if the effect of radiation differed between sites (reflected by a significant interaction between radiation and site). The analyses showed a significant overall radiation effect on abundance of all taxa with the exception of dragonflies and spiders (Table 2). There were significant effects of area on abundance of all taxa with the exception of birds (Table 2). Finally, there were significant differences in radiation effect between areas for four out of six taxa (Table 2). These differences in radiation effect between areas are shown for spiders, butterflies and birds in Fig. 3. Therefore, radiation effects on abundance differed significantly between Fukushima and Chernobyl for a majority of taxa.

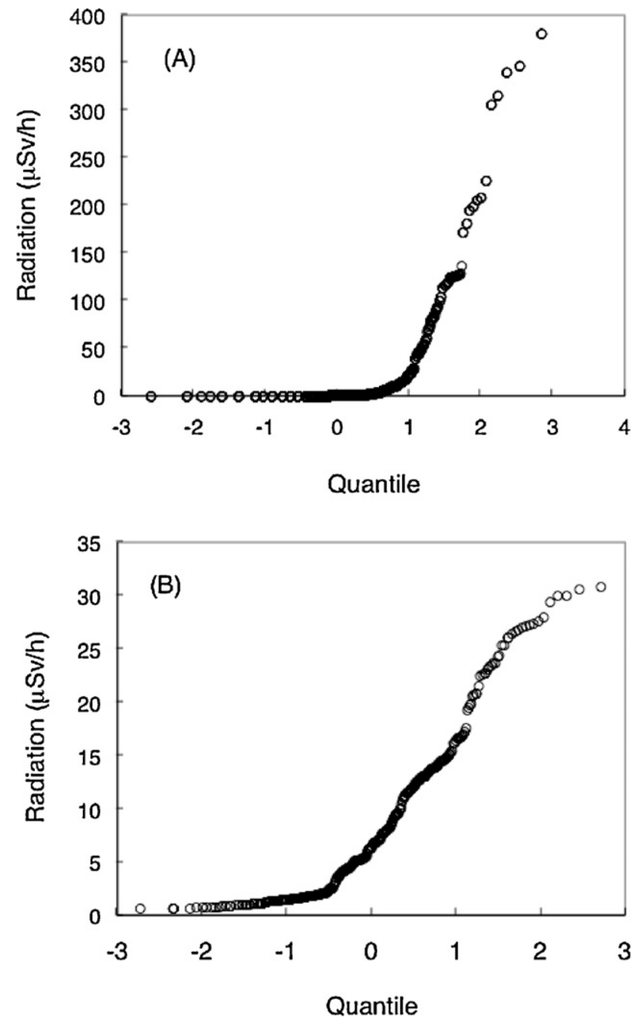

Fig. 2. Normal quantile plots of radiation levels (μSv/h) in (A) Chernobyl and (B) Fukushima.

We found no evidence of the slope of the relationship between abundance of radiation in Fukushima being significantly related to natal dispersal distance ($F = 0.31$, d.f. = 1, 6, $r^2 = 0.05$, $P = 0.60$) or mean population density ($F = 1.39$, d.f. = 1, 6, $r^2 = 0.19$, $P = 0.28$).

4. Discussion

The main findings of this study were that (1) for the regions surveyed, levels of radioactive contamination were higher and less variable at Fukushima-Daiichi than at Chernobyl; (2) the relationship between abundance of animals and radiation was weaker in Fukushima than in Chernobyl; and (3) the relationship between abundance and radiation was more strongly negative in the area with chronic exposure to radiation for many years (Chernobyl) than in the more recently contaminated area (Fukushima). There are no early census data from Chernobyl just after the accident so we cannot directly compare current and past relationships between levels of background radiation and abundance of different taxa of animals. If the relationships between abundance and radiation reported here were caused exclusively by radiotoxicity, we should expect negative relationships in both Chernobyl and Fukushima. That was

Table 1
Species richness of birds and abundance of different animal taxa in Fukushima and Chernobyl in relation to radiation level.

	Sum of squares	d.f.	*F*	*P*	Estimate (SE)
Fukushima					
No. bird individuals	0.775	1, 298	14.89	0.0001	−0.105 (0.027)
No. bird species	0.181	1, 298	6.77	0.010	−0.051 (0.020)
No. bumblebees	0.001	1, 298	0.16	0.69	
No. butterflies	4.553	1, 298	37.18	<0.0001	−0.254 (0.042)
No. cicadas	0.208	1, 298	19.24	<0.0001	−0.054 (0.012)
No. dragonflies	0.127	1, 298	0.87	0.35	
No. grasshoppers	0.004	1, 298	0.22	0.64	
No. spiders	0.636	1, 298	14.12	0.0002	0.095 (0.025)
Chernobyl					
No. mammals	3.669	1, 159	57.28	<0.0001	−0.182 (0.024)
No. bird individuals	6.973	1, 896	256.89	<0.0001	−0.078 (0.005)
No. bird species	4.124	1, 896	172.85	<0.0001	−0.060 (0.005)
No. reptiles	0.093	1, 896	24.14	<0.0001	−0.009 (0.002)
No. amphibians	0.196	1, 896	14.22	0.0002	−0.005 (0.001)
No. bumblebees	1.595	1, 896	55.71	<0.0001	−0.037 (0.005)
No. butterflies	2.153	1, 896	57.63	<0.0001	−0.043 (0.006)
No. dragonflies	1.195	1, 402	34.58	<0.0001	−0.049 (0.008)
No. grasshoppers	0.891	1, 372	13.58	0.0003	−0.071 (0.019)
No. spiders	5.738	1, 896	81.94	<0.0001	−0.071 (0.008)

clearly not what we found. If the relationships were caused by accumulation of mutations following chronic exposure to radiation across generations, we should expect to see more negative effects on abundance in the site with more long-lasting exposure. Consistent with this expectation, we found stronger negative relationships between abundance and radiation in Chernobyl. These findings have important implications for monitoring of the biological effects of radioactive contamination because negative effects are more likely to appear after many generations. Furthermore, we should expect that the negative effects of radiation on abundance of animal taxa in Fukushima to increase over time. We plan to repeat the census in Fukushima in 2011 again in 2012, with the prediction that the abundance should decrease further at the most contaminated census points.

Radioactive contamination may affect the abundance of animals through direct radiotoxic effects on physiology or through indirect effects of mutations that can have deleterious consequences for reproduction and viability. Radioactive contamination may have direct radiation and chemical toxic effects on animals with consequences for survival and reproduction. Previous studies of animals at Chernobyl have shown negative effects of radiation on immunity, antioxidant status, reproductive failure by females and sperm production (see Section 1). Likewise, mutation rates at Chernobyl have increased by up to a factor 20 relative to the normal background mutation rates (Møller and Mousseau, 2006). Here we have tested whether differences in time elapsed since exposure to radioactive contamination may allow discrimination between decreases in abundance due to direct physiological and indirect genetic effects due to mutational load. While the abundance of all animal taxa decreased with increasing level of background radiation at Chernobyl, that was not the case in Fukushima. We emphasize that the census methods were the same in the two areas, and that even the same person conducted all the censuses thereby reducing variance in effects due to inter-observer variability. Møller and Mousseau (2011) have previously shown a high degree of repeatability in census results among years and among countries in studies at Chernobyl, further suggesting that these factors are unlikely to contribute to the results presented here. Several taxa did not show a reduction in abundance with increasing level of background radiation at Fukushima despite the fact that levels of background radiation were higher and less variable at our census points in Fukushima compared to Chernobyl.

We documented differences in effects of radiation on abundance among taxa, and these differences varied between Chernobyl and Fukushima. We found a reduced variance in radiation levels at our census points in Fukushima compared to Chernobyl, and this may have reduced the power of the statistical analyses. However, we note that the negative relationships between species richness and abundance of animals at Chernobyl are not a question of a large variance in levels of background radiation because these relationships were obvious even when making separate analyses for the two halves of the range of radiation (see Fig. 2 in Møller and Mousseau, 2011). In fact, bumblebees, dragonflies and grasshopper were not significantly negatively affected in Fukushima, and the abundance of spiders even increased rather than decreased with level of radiation. We suggest that such differences among species and taxa may be related to ecological characteristics of these taxa (Møller and Mousseau, 2007b, 2011). Detailed studies of birds have shown that species with a high rate of use of antioxidants suffer disproportionately from the effects of radiation on oxidative stress

Table 2
Species richness of birds and abundance of different animal taxa in relation to level of radiation, area (Chernobyl or Fukushima) and their interaction.

Taxon	Radiation (*R*)	Estimate (SE)	Area (*A*)	$R \times A$	Model
No. bird species	33.05***	−0.055 (0.010)	39.50***	0.23	113.95***
No. birds	66.49***	−0.092 (0.011)	0.43	1.45	86.55***
No. bumblebees	4.79*	−0.020 (0.009)	27.76***	3.47	47.46***
No. butterflies	100.27***	−0.149 (0.015)	532.55***	50.39***	223.30***
No. dragonflies	0.03	−0.003 (0.018)	14.83***	6.28*	13.32***
No. grasshoppers	4.69*	−0.032 (0.015)	15.47***	7.05**	22.59***
No. spiders	0.61	0.012 (0.016)	10.17**	28.57***	34.84***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

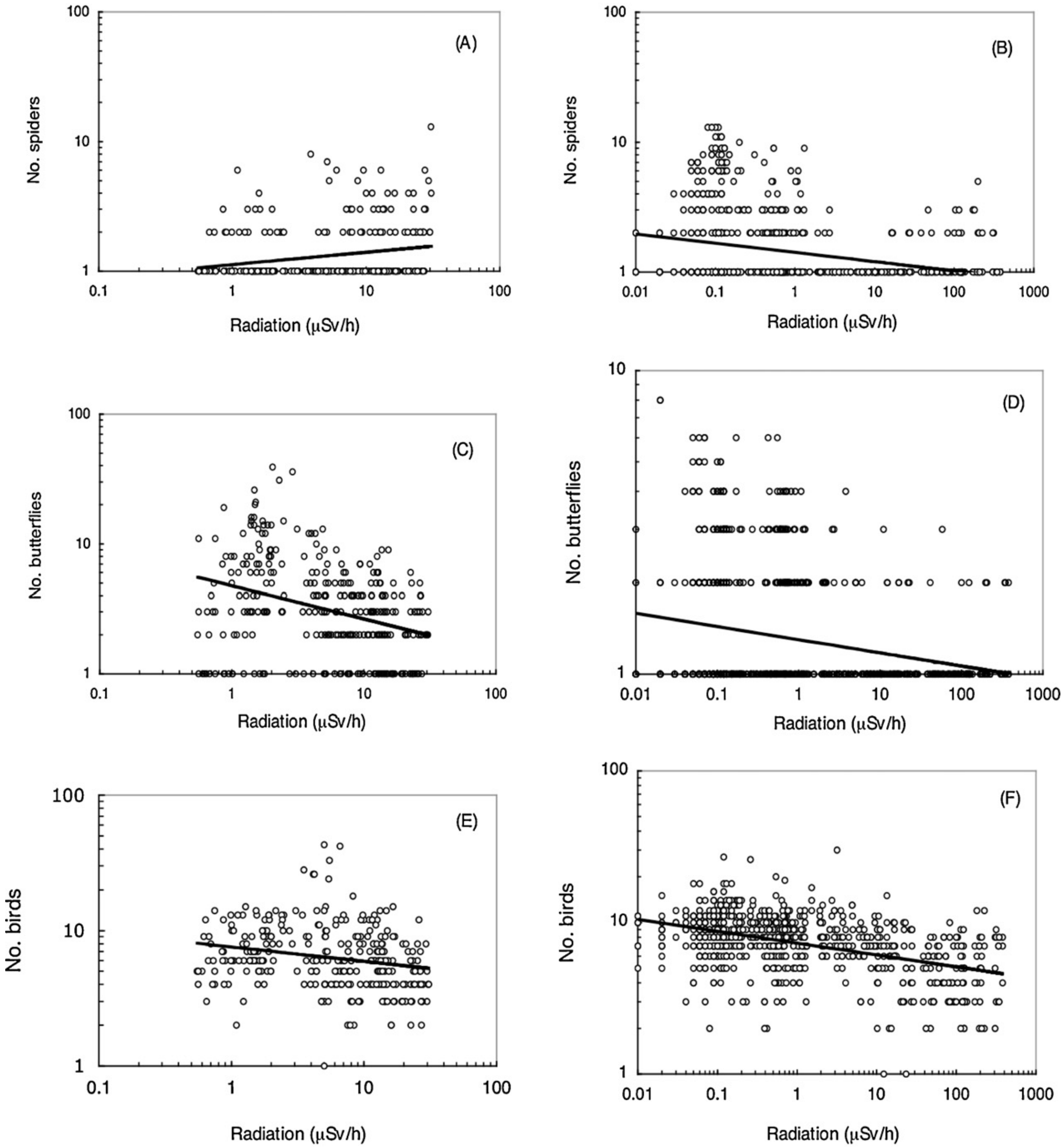

Fig. 3. Abundance of (A, B) spiders, (C, D) butterflies and (E, F) birds in relation to background radiation (μSv/h) in Fukushima (A, C, E) and Chernobyl (B, D, F).

(Møller and Mousseau, 2007b). The increased abundance of spiders at higher levels of radiation in Fukushima may arise from negative effects of radiation on escape ability of insect prey, if prey taxa are more strongly negatively affected by radiotoxicity. We suggest that the initial lack of effect of radiation reported here for several taxa at Fukushima may subsequently change to increasingly suppressed population densities at high levels of background radiation as mutations accumulate. Møller and Mousseau (2011) showed that abundance decreased more at high radiation levels in taxa with long dispersal distances and taxa with high mean population densities in Chernobyl. In Fukushima we found no such evidence of effects of dispersal or population density. Immigration from uncontaminated populations may result in the maintenance of sink populations in contaminated areas (populations that cannot maintain themselves without immigration from elsewhere; Møller et al., 2006), but once the negative effects of radiation appear in populations across large areas, any rescue effect of immigration from source populations is likely to eventually be diminished or disappear.

In conclusion, we have shown that the relationship between abundance of animals and radiation differed significantly between Chernobyl and Fukushima. The correlation between radiation and the abundance of animals were stronger at Chernobyl, where contamination with radioactivity has lasted for 25 years, than at Fukushima, although levels of background radiation generally were much higher at our census points in Fukushima. These results are consistent with the hypothesis that long-term effects of mutation accumulation are more important determinants of abundance than short-term effects of radiotoxicity. The findings reported here have implications for biological monitoring of the effects of radioactive contamination because effects are expected to accumulate over time as a consequence of continuous chronic exposure to radiation. Therefore, any census of long-term effects of radiation on organisms should start from the very beginning of radioactive accidents to allow documentation of trends in populations of animals over time.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2012.06.001.

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