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Efficiency of bio-indicators for low-level radiation under field conditions

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ABSTRACT

Relatively little is known about biological consequences of natural variation in background radiation, and variation in exposure due to nuclear accidents, or even the long term consequences to human health stemming from the over-use of nuclear medicine and imaging technologies (i.e. CAT scans). This realization emphasizes the need for assessment and quantification of biological effects of radiation on living organisms. Here we report the results of an environmental analysis based on extensive censuses of abundance of nine animal taxa (spiders, dragonflies, grasshoppers, bumblebees, butterflies, amphibians, reptiles, birds, mammals) around Chernobyl in Ukraine and Belarus during 2006–2009. Background levels of radiation explained 1.5–26.5% of the variance in abundance of these nine taxa, birds and mammals having the strongest effects, accounting for a difference of a factor 18 among taxa. These effects were retained in analyses that accounted for potentially confounding effects. Effect size estimated as the amount of variance in abundance explained by background level of radiation was highly consistent among years, with weaker effects in years with low density. Effect sizes were greater in taxa with longer natal dispersal distances and in taxa with higher population density. These results are consistent with the hypotheses that costs of dispersal (i.e. survival) were accentuated under conditions of radioactive contamination, or that high density allowed detection of radiation effects. This suggests that standard breeding bird censuses can be used as an informative bio-indicator for the effects of radiation on abundance of animals.

1. Introduction

The biological consequences of natural variation in background radiation levels remain largely unexplored. The average annual worldwide radiation dose is around 2.4 mSv, with a typical range of 1–10 mSv (IAEA, 2006), although variation in background radiation levels varies by more than a factor ten across depending on composition of the underground rock. This variation is associated with significant incidence of cancer and cancer-related mortality in humans (e.g. Lubin and Boice, 1997), testifying to the fact that there may be significant impacts of natural variation in radiation across living beings (e.g. Heidenreich et al., 2000; Moiseev et al., 1973; Pimentel et al., 2003).

Numerous radiation accidents have taken place or been reported, with the total number of radioactive releases worldwide being counted in the hundreds. Although most of these incidents have been minor, more than ten have released large amounts of radioactive material. These include at least three in the former Soviet Union, Three Mile Island in the US and nuclear test sites in the US, Russia, Algeria, China, India, Australia, and the Pacific. To date, the single largest radiation accident is that at Chernobyl on 26 April 1986 that resulted in the emission of at least 9.35×10^3 to 1.25×10^4 peta-Becquerels to the environment (Yablokov et al., 2009). The most important isotopes and their half-lives were iodine (^{131}I, 8 days), strontium (^{90}Sr, 29 years), cesium (^{137}Cesium, 30 years) and plutonium (^{239}Pu, 24,110 years). Coincidentally, the soils of northern Ukraine have some of the lowest levels of natural background radiation in the world at around 0.02–0.03 μSv/h (Ramzaev et al., 2006) making the Chernobyl fallout particularly apparent in this part of the world, but also making the consequences particularly severe due to lack of adaptation to background radiation.

Given our generally poor knowledge of the effects of these two causes of radiation on the biota there has been surprisingly little study of the biological consequences (Møller and Mousseau, 2006, 2008, 2009). The notion that low-level radiation has an effect on the abundance or performance of animals is controversial due to the difficulty of extrapolating from high level to low-level exposure (e.g. Chadwick et al., 2003; Moss et al., 2006; Tubiana et al., 2006), as are the effects of low-level radiation on disease including cancer (e.g. Brenner et al., 2003; Prasad et al., 2004). For example,

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exposure to chronic and acute radiation has different effects (e.g. Wickliffe et al., 2003). Numerous laboratory studies have investigated effects of radiation on model systems including cell cultures (e.g. Chadwick et al., 2003; Liang et al., 2007; Sykes et al., 2006). Laboratory model systems traditionally utilize controlled environmental conditions, but also providing benign and ad libitum access to food and other resources. In contrast, field assessment of biological effects of low-level radiation relies on the fact that environmental conditions in the field typically are sub-optimal in terms of food, predation risk, and risk of parasitism, and animals typically have to work hard to meet their requirements (review in Møller et al., 1998). For example, carotenoids and other antioxidants are typically limiting under field conditions (e.g. Møller et al., 2000), with important consequences for free radical scavenging and ultimately for damage to DNA and other biologically significant molecules (e.g. Halliwell and Gutteridge, 1999; Leffler, 1993). Radiation increases the level of oxidative stress (e.g. Bonisoli-Alquati et al., 2010a,b; Bazhan, 1998; Ben-Amotz et al., 1998; Chaialo et al., 1991; Ivaniota et al., 1998; Kumerova et al., 2000; Lykholat and Chernaya, 1999; Neyfakh et al., 1998a,b). Thus, species that use antioxidants for biological needs other than free radical scavenging caused by radiation such as deposition in eggs and plumage and use during migration and dispersal have been found to suffer the most from elevated levels of background radiation (Møller and Mousseau, 2007b). Several studies have indicated that the presence of high levels of carotenoids may reduce mutation rates (reviews in Ferguson, 1994; Krinsky and Denek, 1982; Møller et al., 2000; Sies, 1993; Valko et al., 2004). We might also consider that mildly deleterious mutations will have benign effects under lab conditions, but more serious consequences under adverse environmental conditions. This line of argument suggests that biologically relevant estimates of effects of low-level radiation are best obtained from free-living organisms under natural environmental conditions. This also raises the possibility of using standard census techniques (e.g. Voříšek et al., 2010) for assessment of effects of low-level radiation on free-living organisms.

The primary objective of this study was to identify biological indicator(s) of background radiation level. To this end we conducted extensive field censuses of nine different animal taxa in the surroundings of Chernobyl in Belarus and Ukraine during 2006–2009, with some of these results already having been published. Because many different biotic and abiotic environmental factors can affect census results, we also recorded biotic and abiotic factors known to potentially influence census results and entered these into statistical models describing the relationship between abundance and level of background radiation. A second objective was to test the repeatability of radiation effects on abundance among years. A third objective was to test the extent to which natal dispersal and mean population density affected the relationship between radiation and abundance. Three possible scenarios were set out a priori for dispersal: Either dispersal may bring immigrants to suitable habitat with low population density thereby obscuring any relationship between radiation and abundance or, dispersal may permit individuals to escape locally deleterious conditions. Alternatively, dispersal may be costly in terms of production of free radicals from physical activity and/or from immune response to novel antigens (Møller and Mousseau, 2007b). Similar effects have been reported in many other taxa (Møller et al., 2000). Given that antioxidants used for neutralizing free radicals may be used to eliminate the negative effects of radiation on general health and on mutations in particular (e.g. Bazhan, 1998; Ben-Amotz et al., 1998; Chaialo et al., 1991; Ivaniota et al., 1998; Kumerova et al., 2000; Lykholat and Chernaya, 1999; Neyfakh et al., 1998a,b; Bonisoli-Alquati et al., 2010b), taxa with long-distance dispersal are predicted to suffer more from such costs (i.e. antioxidant limitation) than taxa with short dispersal distances. Low levels of abundance will invariably prevent detection of strong effects for statistical reasons because small mean values generally are associated with small variances. Therefore, it is crucial to include data for several years to ensure that the abundance estimates exceed low mean abundances.

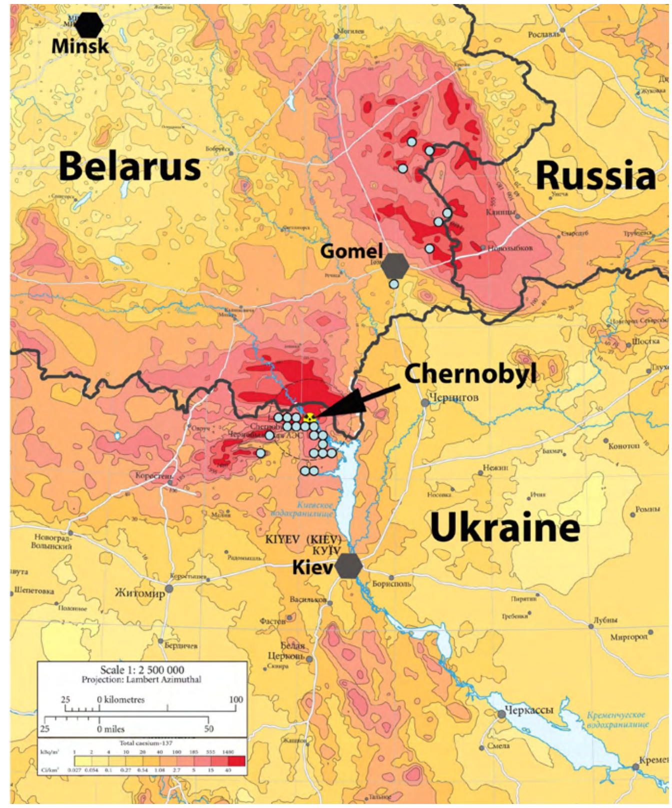

Fig. 1. Location of census areas and levels of background radiation around Chernobyl. Partly developed from European Union (1998).

2. Methods

2.1. Study sites

APM (wearing a radiation protection suit in the most contaminated areas) conducted standard point counts during 29 May–9 June 2006, 1–11 June 2007, 29 May–5 June 2008 and 1–6 June 2009, with each count lasting 5 min during which the number of spider webs, and the number of individual grasshoppers, dragonflies, bumblebees, butterflies, amphibians, reptiles and birds seen or heard were recorded (Møller, 1983; Bibby et al., 2005). The census was conducted within the Chernobyl Exclusion Zone or in areas adjacent on the southern and western borders with a permit from the Ukrainian authorities and in areas in southern Belarus around Gomel (breeding seasons 2006–2009) (Fig. 1). A total of 254 points (breeding season 2006), 235 points (breeding season 2007), 237 points (breeding season 2008) and 159 points (breeding season 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)). All sampling sites were identified using GPS coordinates, and samples for 159 sites were recorded in all four years.

We censused birds at the end of May and the beginning of June when most individuals reach their annual maximum of singing activity, making censuses of breeding birds highly reliable (Voříšek et al., 2010). We directly tested the reliability of our counts by letting two persons independently perform counts. The degree

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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). To avoid counting the same individual repeatedly we only counted the minimum number of individuals recorded simultaneously. For example, if the tracks of a fox *Vulpes vulpes* crossed the transect to the right, and 30 m later the tracks of a fox crossed to the left, this was only counted as a single individual, although two individuals may have been involved on some such occasions. In contrast, if the tracks of two foxes crossed to the left, while none crossed to the right, this was counted as two foxes.

2.2. Confounding habitat and weather variables

Abundance estimates can be affected by numerous confounding variables (Voříšek et al., 2010), and, therefore, it is crucial 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 these different habitat types within a distance of 50 m from the observation point. Agricultural habitat included edges between forest and open areas, and the agricultural habitat variable thus also reflected the amount of edge habitat between forest and open areas. Maximum height of trees was estimated to the nearest 5 m and soil type was recorded as loam/clay or sand. The presence of open water within a distance of 50 m was also recorded. 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, range 0–1 during the censuses), temperature (degrees Celsius, range 12–25 °C), and wind force (Beaufort, range 0–4 during the censuses). 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 bird (Voříšek et al., 2010), and higher levels of activity for thermo-philic vertebrates and invertebrates, we also included time squared as an explanatory variable.

2.3. Measuring background radiation levels

We measured radiation levels in the field and cross-validated these with measurements by the Ministry of Emergencies and Shestopalov (1996). We measured α, β, and γ radiation at ground level at each census point after having conducted the census (thus making the census blindly with respect to radiation level) using a hand-held dosimeter (Model: Inspector, SE International, Inc., Summertown, TN, USA). We measured levels several (2–3) times at each site and averaged the measurements. Our data were validated with correlation against data from the governmental measurements published by Shestopalov (1996), estimated as the mid-point of the ranges published, with analyses showing a high degree of consistency between methods (Møller and Mousseau, 2007a). Radiation levels vary greatly at a local scale due to heterogeneity in deposition of radioactive material after the Chernobyl accident (Fig. 1; Shestopalov, 1996). Our measurements at the census points ranged from 0.01 to 135.89 μSv/h.

2.4. Dispersal distance

We do not have comparable estimates of dispersal distances for different taxa. Therefore, we asked 12 biologists to score the natal dispersal distance of the different taxa on a scale from 0 to 100, with 100 being given to birds. This was done blindly without any prior information on the purpose of the study. There was a highly significant repeatability of these scores ($F = 4.19$, d.f. = 11,96, $P < 0.0001$), implying that different persons ranked the animal taxa similarly with respect to perceived natal dispersal ability. Thus we used the mean scores in the subsequent analyses. Means (SE) are reported in Appendix A.

2.5. Mean population density

We used the mean number of individuals recorded per census point as an estimate of population density. We do not consider point counts to provide reliable information on absolute abundance. However, they should provide information on relative abundance because different taxa should be similarly detectable across sites (Voříšek et al., 2010). Such relative abundance would suffice for our purposes. We note that such information is unavailable for most of the taxa investigated here.

2.6. Statistical analyses

Radiation level and abundance were $\log_{10}$-transformed, while ground coverage with farmland and deciduous forest was square root arcsine-transformed (coniferous forest was not included as an explanatory variable, because it simply represents the ground coverage not attributed to farmland and deciduous forest). 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, 2000).

We quantified the relationship between abundance of different taxa and level of radiation by estimating the coefficient of determination and by calculating the slope of the relationship between abundance and $\log_{10}$-transformed radiation. These slopes were used for subsequent analyses.

As a measure of effect size we used R^2 because it directly reflects the amount of variance explained. We square root arcsine-transformed R^2 to obtain an approximately normal distribution.

We tested for consistency in results by testing the relationship between effect sizes before and after accounting for the potentially confounding variables. Likewise, we tested for consistency in effect size among years in a one-way ANOVA with taxon as a factor.

3. Results

Effects of background radiation on nine animal taxa are reported in Table 1. All effects were statistically significant. R^2 ranged from 0.015 in amphibians to 0.265 in mammals with considerable scatter around the regression lines (Fig. 2).

In a second series of models we entered potentially confounding factors such as time of day, time of day squared, cloud cover, temperature, soil type, cover with grassland and shrub, cover with forest, height of trees, and presence of water. Effect sizes differed little from the first series of analyses with values ranging from 0.006 in butterflies to 0.196 in mammals (Table 2). There was a strong positive correlation between R^2 values for the two sets of analyses ($F = 17.02$, d.f. = 1,7, $R^2 = 0.71$, $P = 0.0044$, slope (SE) = 0.79 (0.19)), with mean values not significantly different (paired t-test, $t = 2.02$, d.f. = 8, $P = 0.08$). Effect sizes tended to be stronger when the relationships were controlled for potentially confounding variables.

There was significant consistency in R^2 among years, with taxon accounting for 61% of the variance in effect size (Table 2; $F = 4.91$, d.f. = 6,19, $R^2 = 0.61$, $P = 0.0035$). Differences in effect size among

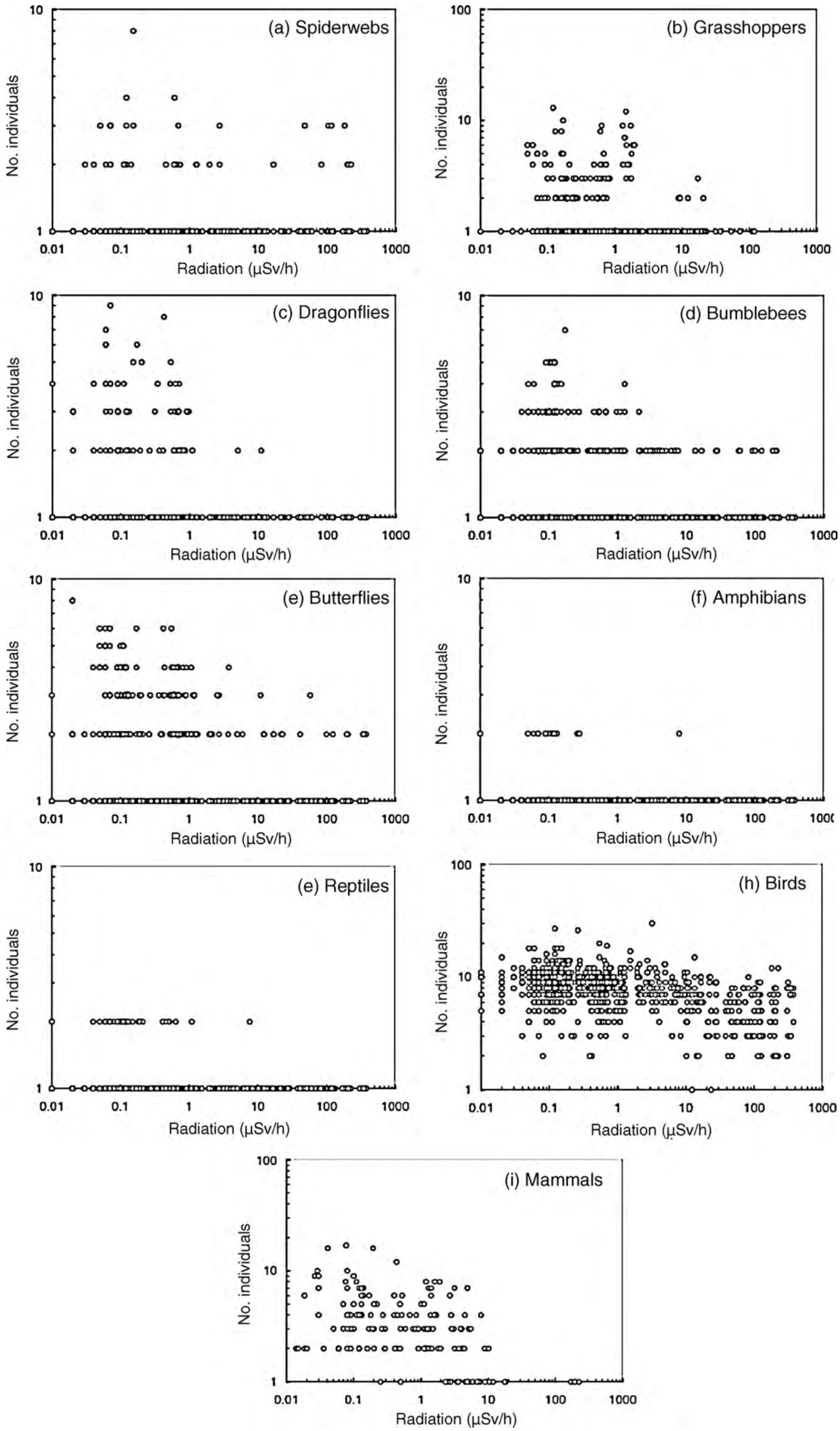

Fig. 2. Abundance of nine taxa of animals in relation to levels of background radiation (μSv/h) around Chernobyl. (a) Spider webs, (b) grasshoppers, (c) dragonflies, (d) bumblebees, (e) butterflies, (f) amphibians, (g) reptiles, (h) birds and (i) mammals.

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Table 1
Models relating abundance of different animal taxa to background radiation levels. Slope (SE) reflects the relationship between $\log_{10}$-transformed abundance (+1) and $\log_{10}$-transformed radiation level (μSv/h).

Taxon	*F*	d.f.	R^2	*P*	Slope	SE
Spiderwebs	81.94	1,896	0.084	<0.0001	−0.162	0.018
Grasshoppers	13.58	1,372	0.035	<0.0001	−0.071	0.019
Dragonflies	34.58	1,402	0.079	<0.0001	−0.112	0.019
Bumblebees	55.71	1,896	0.059	<0.0001	−0.085	0.011
Butterflies	57.63	1,896	0.060	<0.0001	−0.099	0.013
Amphibians	14.22	1,896	0.015	0.0002	−0.005	0.001
Reptiles	24.13	1,896	0.026	<0.0001	−0.021	0.004
Birds	258.21	1,896	0.224	<0.0001	−0.094	0.006
Mammals	57.27	1,159	0.265	<0.0001	−0.182	0.024

Table 2
Models relating abundance of different animal taxa to background radiation levels after accounting for the confounding effects of time of day, weather, and habitat. Slope (SE) reflects the relationship between $\log_{10}$-transformed abundance (+1) and $\log_{10}$-transformed radiation level (μSv/h).

Taxon	*F*	d.f.	R^2	*P*	Slope	SE
Spiderwebs	98.45	1,886	0.100	<0.0001	−0.070	0.007
Grasshoppers	21.42	1,364	0.056	<0.0001	−0.098	0.021
Dragonflies	10.47	1,393	0.026	0.0013	−0.038	0.012
Bumblebees	70.30	1,886	0.074	<0.0001	−0.051	0.006
Butterflies	5.59	1,886	0.006	0.018	−0.016	0.007
Amphibians	6.66	1,886	0.007	0.010	−0.004	0.002
Reptiles	13.02	1,886	0.014	0.0003	−0.009	0.002
Birds	131.98	1,883	0.130	<0.0001	−0.083	0.007
Mammals	37.32	1,153	0.196	<0.0001	−0.192	0.031

years were significantly accounted for by density, with effect sizes being lower in years with lower density (effect of density within taxon, nested ANOVA: $F = 3.06$, d.f. = 7,12, $R^2 = 0.86$, $P = 0.043$), as expected for least squares statistical procedures (Table 3).

There was a strong positive relationship between mean population size and the efficiency of abundance of different taxa as an indicator of radiation levels (i.e. effect size) (Fig. 3a; $F = 14.64$, d.f. = 1,7, $R^2 = 0.67$, $P = 0.00065$, slope (SE) = 0.0526 (0.0138)). In addition, there was a strong negative relationship between mean dispersal distance score and effect size among taxa (Fig. 3b; $F = 16.55$, d.f. = 1,7, $R^2 = 0.70$, $P = 0.0048$, slope (SE) = −0.0825 (0.0203)). Mean density and dispersal score were strongly positively correlated ($F = 42.35$, d.f. = 1,7, $R^2 = 0.86$, $P = 0.0003$, slope (SE) = 1.425 (0.219)). This implies that we could not investigate the independent effect of the two predictors because of collinearity.

4. Discussion

The main findings of this study of animal taxa as bio-indicators of low-level radiation in Ukraine and Belarus were that taxa differed considerably in suitability, with effect size varying by more than two orders of magnitude, birds and mammals showing the strongest effects of radiation on abundance. Potentially confound-

Table 3
Consistency in relationships between abundance of different animal taxa and background radiation level in different years. Slope (SE) reflects the relationship between $\log_{10}$-transformed abundance (+1) and $\log_{10}$-transformed radiation level (μSv/h).

Taxon	Year	*F*	d.f.	R^2	*P*	Slope	SE
Spiderwebs	2006	27.06	1,252	0.10	<0.0001	−0.022	0.003
Spiderwebs	2007	4.24	1,238	0.02	0.041	−0.024	0.012
Spiderwebs	2008	0.06	1,235	0.00	0.81	−0.002	0.008
Spiderwebs	2009	1.60	1,165	0.01	0.21	0.009	0.007
Dragonflies	2008	14.74	1,235	0.06	0.0002	−0.046	0.012
Dragonflies	2009	20.70	1,165	0.11	<0.0001	−0.051	0.011
Bumblebees	2006	89.76	1,252	0.26	<0.0001	−0.096	0.010
Bumblebees	2007	7.53	1,238	0.03	0.0065	−0.025	0.009
Bumblebees	2008	0.37	1,235	0.00	0.54	−0.005	0.008
Bumblebees	2009	0.11	1,165	0.00	0.74	−0.003	0.009
Butterflies	2006	54.27	1,252	0.18	<0.0001	−0.076	0.010
Butterflies	2007	5.07	1,238	0.02	0.025	−0.029	0.013
Butterflies	2008	5.13	1,235	0.02	0.024	−0.026	0.012
Butterflies	2009	6.54	1,165	0.04	0.011	−0.026	0.010
Amphibians	2006	4.73	1,252	0.02	0.031	−0.006	0.003
Amphibians	2007	4.77	1,238	0.02	0.030	−0.006	0.003
Amphibians	2008	1.42	1,235	0.01	0.23	−0.002	0.002
Amphibians	2009	4.15	1,165	0.02	0.043	−0.005	0.003
Reptiles	2006	9.63	1,252	0.04	0.0021	−0.012	0.004
Reptiles	2007	4.00	1,238	0.02	0.047	−0.006	0.003
Reptiles	2008	5.73	1,235	0.02	0.017	−0.010	0.004
Reptiles	2009	5.14	1,165	0.03	0.025	−0.008	0.004
Birds	2006	144.43	1,252	0.36	<0.0001	−0.130	0.011
Birds	2007	176.71	1,238	0.43	<0.0001	−0.141	0.011
Birds	2008	102.36	1,235	0.28	<0.0001	−0.103	0.012
Birds	2009	25.62	1,163	0.14	<0.0001	−0.064	0.013

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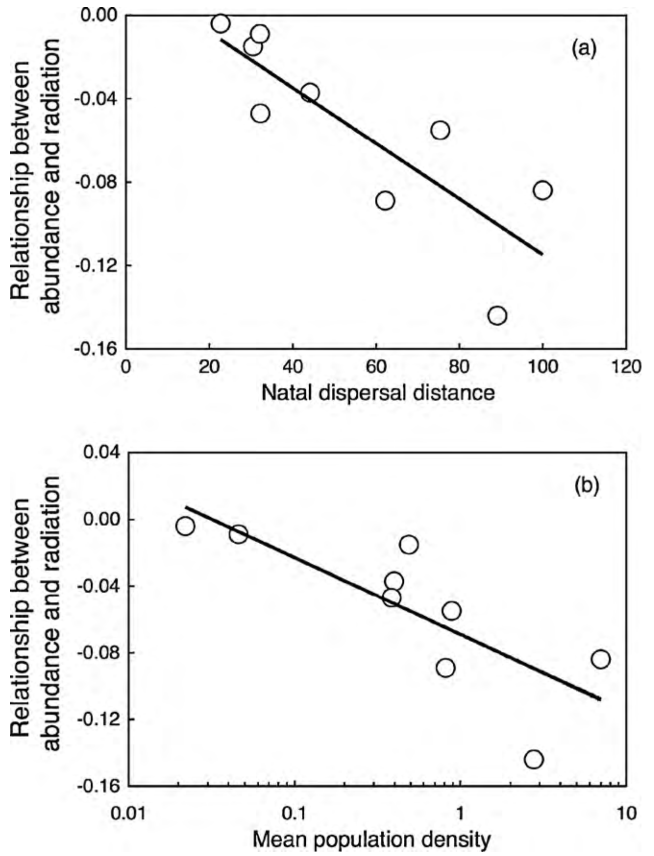

Fig. 3. Effect size of the relationship between abundance and background radiation level in different animal taxa in relation to (a) their natal dispersal ability (arbitrary units) and (b) mean population density (number of individuals per census point). The lines are the linear regression lines.

ing variables did not qualitatively affect the results. Finally, taxa with long natal dispersal distances and high population densities showed stronger negative relationships with radiation than taxa with short dispersal and smaller densities.

The strength of the association between abundance of different taxa of animals and background radiation level varied by more than a factor ten. These findings are consistent with the hypothesis that low-level radiation has significant negative impact on population of animals. This is a significant finding because negative impacts of radiation on physiology or reproductive success, as reported repeatedly (e.g. Heidenreich et al., 2000; Moiseev et al., 1973; Pimentel et al., 2003), will not necessarily have population consequences. Clearly, there were significant differences among taxa in effects of radiation on abundance, and these differences were consistent among years, suggesting that even a census based on a single year will provide reliable information on effects of radiation on abundance. The different amounts of variance explained suggest that mammals and birds are particularly susceptible to radiation and hence particularly suitable for censusing the effects of radiation on animals, followed by spiderwebs, bumblebees and grasshoppers. Because mammals are difficult and time consuming to census, with the only exception being censuses of tracks in snow, birds appear to be the most efficient indicator of low-level radiation. Because birds are generally abundant, distributed everywhere, and relatively easy to identify and count, they potentially provide an effective tool for censuses directed towards understanding effects of radiation on abundance of animals. Dragonflies, butterflies, amphibians and reptiles were the least efficient bioindicators of low-level radiation. The reason for such differences in susceptibility to radiation among taxa remains poorly understood. However, Møller and Mousseau (2007b) showed for birds that interspecific differences in availability and/or use of antioxidants may play an important role in determining effects of radiation on abundance. Such analyses may also be feasible for insects or other taxa with high metabolic rates for their body size.

Many potentially confounding variables may influence census results (reviews in Voříšek et al., 2010). Here we explicitly tested the effect of time of day, weather and several habitat variables on the abundance of nine animal taxa. Effect sizes, quantified as R^2, were consistent between estimates that accounted or did not account for potentially confounding variables. Hence, the biological signal in abundance data is so strong that potentially confounding variables only marginally affected effect size estimates, although there was a weak, but non-significant reduction in effect size when confounding variables were not considered.

Dispersal may be an important factor affecting the association between abundance of animals and level of background radiation. We hypothesized two different scenarios: A first possibility is that dispersal is costly in terms of production of free radicals from physical activity due to actual dispersal and/or from immune response to novel antigens encountered in the new environments during dispersal (Møller and Mousseau, 2007b). A second possibility is that dispersal obscures any relationship between abundance and low-level radiation due to immigration from elsewhere. The relationship that we found is consistent with the first hypothesis because effect size was strongly negatively related to dispersal distance (Fig. 3a). Thus, taxa with long dispersal distances showed the strongest effect sizes, while taxa with smaller dispersal abilities only showed weak effects. However, we also found that taxa with high mean densities showed stronger effects than taxa with low densities (Fig. 3b). This relationship is expected because small mean values generally are associated with small variances.

This paper describes patterns of abundance of different animal taxa in relation to radiation, but does not directly investigate the underlying mechanisms. Radioactive fallout from Chernobyl is associated with reduced and suppressed reproduction, reduced reproductive success and reduced nestling and adult survival rate (Møller and Mousseau, 2007b; Møller et al., 2008; Yablokov et al., 2009). Such negative effects will across generations tend to suppress local population densities in the most contaminated areas unless balanced by immigration. Previous studies of dispersal and radiation have shown that avian species with long-distance dispersal are the most sensitive to radiation (Møller and Mousseau, 2007b). Thus immigration is an unlikely factor maintaining local population density in the most contaminated areas. Source-sink dynamics may stabilize population densities in radioactively contaminated areas if radioactive population sinks receive immigrants from non-radioactive population sources that have a net production of emigrants. While such dynamics have been described for Chernobyl (Møller et al., 2006), we consider immigration from population sources as inadequate for maintaining stable populations in contaminated areas.

In conclusion, extensive census data for nine taxa of animals vary considerably in efficiency as predictors of background radiation levels. Furthermore, taxa with long dispersal distances showed stronger relationships with radiation than taxa with short dispersal distances. Finally, the most abundant taxa showed the largest effect sizes. We recommend that these results be validated by precise data on individual internal doses. Our findings have implications for choice of organisms for estimating the effects of low-level radiation on the abundance of free-living organisms.

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Appendix A.

Natal dispersal scores for different animal taxa based on scores provided by 12 scientists. The value for birds was set to 100.

Taxon	Mean natal dispersal	SE natal dispersal	Mean population density per census point
Birds	100.0	–	7.010
Mammals	89.1	11.7	2.764
Spiders	75.4	25.8	0.885
Grasshoppers	62.2	18.2	0.816
Dragonflies	44.1	16.1	0.399
Bumblebees	32.3	8.5	0.489
Reptiles	32.1	9.0	0.046
Butterflies	30.5	6.9	0.489
Amphibians	22.7	6.5	0.022

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