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Assessing effects of radiation on abundance of mammals and predator–prey interactions in Chernobyl using tracks in the snow

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ABSTRACT

To test whether radioactive contamination reduced the abundance of mammals, and whether species differed in susceptibility to radiation, we censused mammals by counting tracks in the snow along 161 100-m line transects around Chernobyl during February 2009. The abundance of mammal tracks was negatively related to level of background radiation, independent of the statistical model, with effects of radiation accounting for a third of the variance. The effect of radiation differed significantly among species. There was a positive relationship between abundance of predators and abundance of prey, modified by the level of background radiation because the number of predators increased disproportionately with the number of prey at high levels of radiation. These findings suggest that predatory mammals aggregate in areas with abundant prey, especially when prey are exposed to high levels of radiation. This study emphasizes the negative effects of level of background radiation on the abundance of mammals and predator–prey interactions.

1. Introduction

Radioactive contamination occurs naturally to varying extent or due to accidental release of radionuclides into the environment. Although a large number of accidents has taken place around the world (Sovacool, 2010), by far the largest release occurred at Chernobyl on 26 April 1986, when radioactive material hundreds of times the amount contained in the nuclear bombs in Hiroshima and Nagasaki were released into the environment (Shestopalov, 1996). The effects of this event on free-living organisms and humans still remain poorly known mainly due to a general lack of research (Møller and Mousseau, 2006; von Wehrden et al., 2012).

Surprisingly, there has been no concerted effort to quantify the relationship between abundance of animals and plants and background level of radiation, and, therefore, the effects of radiation from Chernobyl on fauna and flora remain to be determined. Recently, extensive censuses have revealed negative relationships between the abundance of a range of animals and the level of background radiation around Chernobyl, Ukraine (Møller and Mousseau, 2007a, 2009a,b), and similar patterns have been described from Belarus (Møller and Mousseau, 2007a, 2009a,b). The negative relationships between abundance and radiation were present in mammals, birds, bumblebees, butterflies, dragonflies, grasshoppers and spiders (Møller and Mousseau, 2007a, 2009a,b, 2011). We have also described negative relationships between species richness of birds and level of background radiation (Møller and Mousseau, 2007a). These patterns were present even when controlling statistically for differences in habitat, soil quality, weather conditions that could affect abundance estimates, and time of day. We are unaware of any other studies covering more than a few sampling sites suggesting that there are no effects of radiation on abundance or species diversity.

Extensive censuses of animals and plants have the added advantage that they allow for statistical tests of interspecific differences in susceptibility to radiation. Such tests provide the opportunity to investigate ecological factors that predict interspecific differences in susceptibility and identification of underlying mechanisms. Møller and Mousseau (2007b) provided the first such study, using extensive breeding bird surveys to tests for factors associated with a negative impact of radiation on abundance.

The objectives of the present study were to test if the abundance of snow tracks and by implication the abundance of mammals in contaminated areas around Chernobyl is a reliable predictor of external level of background radiation (Møller and Mousseau, 2011). Although censuses of mammals based on snow tracks are a standard procedure in ecological studies (e.g. Beauvais and Buskirk, 1999; Hansson, 1994; Rhim and Lee, 2007), this (or any other) method has never been used in Chernobyl. We tested the following four predictions: (1) The abundance of mammals is negatively related to the level of radiation, even after controlling statistically for potentially confounding variables, as expected if radiation reduces fecundity, survival rate and the abundance of food. (2) The

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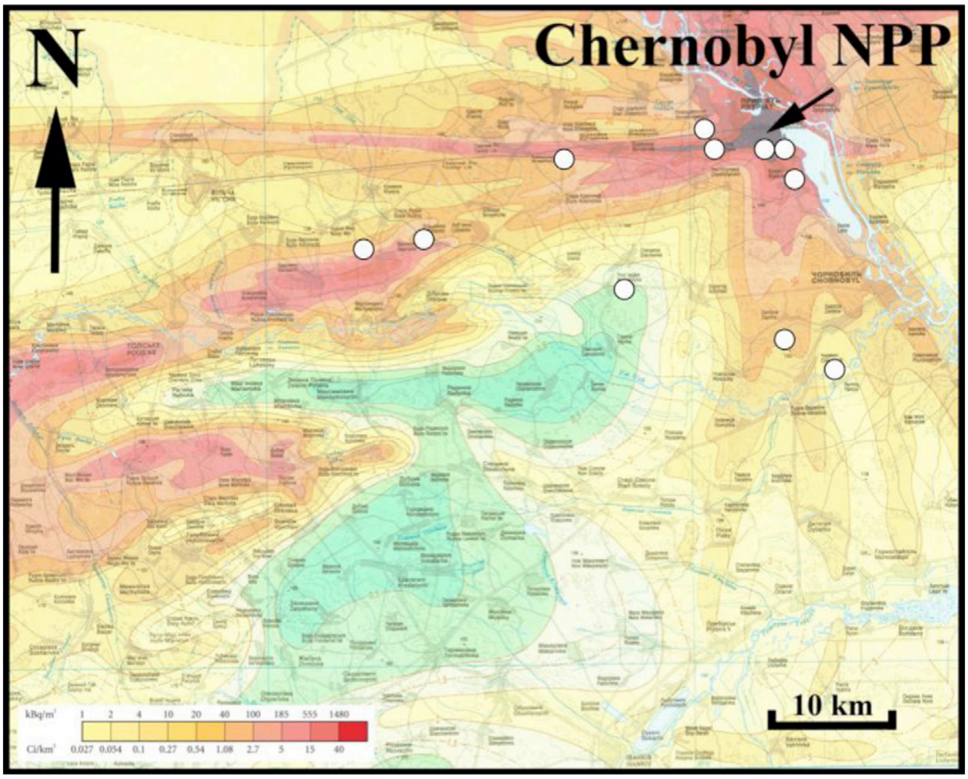

Fig. 1. Study sites used for censusing mammals in the area around Chernobyl and level of background radiation (darker colors imply higher levels of radiation). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)
Modified from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

effect of radiation on abundance of mammals differs among species. Such an interspecific difference in effect of radiation on abundance would be expected because radiation is a source of oxidative stress and species differ in their use of antioxidants. Thus, species of birds that use more antioxidants for their normal activities show a greater reduction in abundance in areas with high levels of ionizing radiation (e.g. Møller and Mousseau, 2007b). (3) The abundance of predators is positively related to the abundance of prey due to a functional response, with a disproportionate number of predators occurring at high levels of radiation because the negative effects of radiation make prey in such areas particularly susceptible to predation. We tested these predictions by analyzing data collected from 161 line transects conducted inside or just outside the Chernobyl exclusion zone in Ukraine in 2009.

2. Materials and methods

2.1. Study sites

The study sites were situated inside or just outside the exclusion zone of Chernobyl (Fig. 1). Sites along roads or paths were chosen to have a wide range of radiation, varying by more than four orders of magnitude. The Chernobyl exclusion zone and the surrounding areas show a patchwork of radiation with a high degree of spatial heterogeneity. Therefore, it is fully feasible to choose neighboring study areas that differ in level of background radiation by more than two orders of magnitude (Fig. 1). We made an exhaustive survey of 11 study areas that covered this spatial heterogeneity in background radiation to ensure that neighboring sites had both low and high levels of radiation to ensure that other confounding variables would not affect our conclusions. Still, we recorded a number of environmental variables other than level of background radiation (see Section 2.2) to make an effort to statistically control for any such confounding effects. The 11 study areas are separated by a maximum distance of 43 km, and they cover an area of 800 km^2.

2.2. Transects

Using tacks in snow as an estimate of abundance of animals is an old method that has been adopted in many studies (e.g. Beauvais and Buskirk, 1999; Hansson, 1994; Rhim and Lee, 2007). Census data can be adjusted for time that tracks have accumulated (i.e. time since last snowfall), although variation in visibility and persistence of tracks among species and sites may also be important (Beauvais and Buskirk, 1999). Here we conducted transects during a short time period of 1.5 days thereby avoiding the possibility that tracks accumulated over time or they deteriorated in quality and hence information content over time. Our extensive effort to cover a large number of sites and habitats differing in level of background radiation assured that we covered all habitats relative to their abundance in the study sites, but also showed that such a study of general scientific interest is fully feasible within a short window of opportunity.

APM conducted 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 immediately following heavy snowfall in the early morning (Fig. 1). Each transect was separated from others by a minimum distance of 50 m, with most being separated by distances of 100–500 m. We were unable to make line transects before 3 February because of a deficit of snow, and snow melt on 4 February, combined with little snow fall in some areas, prevented line transects after 12:00 due to lack of visibility of tracks. We had previously attempted to study mammal tracks in relation to the level of background radiation during a week of field work in December 2007, but we were unable to make line transects because the snow melted as we landed in Kiev.

Transects for the present study were made during intensive fieldwork only lasting 1.5 days. Therefore, we consider that there was little opportunity for tracks to accumulate over time. Indeed, when we entered time since last snowfall as a predictor in our statistical models (see Section 3), this variable only had a marginal importance as a predictor. This justifies our assumption that tracks were largely made during a single bout of activity with little or no opportunity for the same mammals to make repeated tracks over time. Even if there were accumulation of tracks over time, the number of tracks would still reflect mammal activity and hence be a function of actual abundance at a given site. Although the total number of 161 transects was arbitrary due to constraints imposed by changes in weather, such a large number of transects allows for a very high statistical power given a significance level of 5%. Thus, for a large effect size explaining 25% of the variance, as we recorded in our study, the statistical power was 1.00 with 95% confidence limits of 0.9998–1.0000.

APM identified for each transect all mammal tracks in the snow using the field guide by Bang and Dahlstrøm (2001). To avoid counting the same individual repeatedly we only counted the minimum number of individuals recorded simultaneously in a given transect. 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.

We recorded for each transect within a distance of 100 m the percentage cover with grass, bushes and trees to the nearest 5%. It snowed heavily between 2 and 4 a.m. on 3 February, and we recorded time since this last snowfall because more tracks accumulate with time (Beauvais and Buskirk, 1999; Hansson, 1994; Rhim and Lee, 2007), starting our first census at 9:00 a.m. on 3 February when light conditions allowed reliable identification of tracks. Because the snow was fresh, there were no problems of seeing or identifying tracks.

2.3. Radiation levels

Once having finished a line transect we measured α, β and γ radiation 2–3 times at ground level using a hand-held dosimeter (Model: Inspector, SE International, Inc., Summertown, TN, USA). Cross-validation against data from Shestopalov (1996) revealed a strong positive relationship (linear regression on log–log transformed data: $F_{1,252} = 1546.49$, $r^2 = 0.86$, $P < 0.0001$, slope (SE) = 1.28 (0.10)), suggesting reliability of our estimates of background radiation.

The entire data set is reported in Appendix 1.

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2012.10.025.

2.4. Statistical analyses

Radiation and body mass were $\log_{10}$-transformed, while coverage with grassland, shrub, and forest was square root arcsine-transformed before analyses in order to obtain normal distributions.

All analyses were made with the statistical software JMP (SAS, 2012). For each species we used number of individuals at each of the 161 transects as the dependent variable and the habitat variables, time since last snowfall and radiation level as independent variables, using a Poisson error distribution. We tested for an effect of radiation by including radiation level, species and the radiation by species interaction as an estimate of differences in effect among species.

We tested for a functional response of predators to prey abundance by relating the abundance of predators to the abundance of prey, the squared abundance of prey, level of radiation, and the interactions between level of radiation and abundance of prey and squared abundance of prey, respectively. This model also initially included time since last snowfall as an additional predictor variable.

We had a variable number of transects per site for logistic reasons, and this could potentially cause bias in the estimates. Therefore, we developed random effect models for the models reported in Tables 1 and 4 by including site as a random factor. We did not make a random model for the analysis in Table 3 because random and nested effects cannot be included in the same model.

We estimated an effect size of the relationship between abundance and radiation level from the *F*-statistics of the partial regression by transforming these into Pearson product-moment correlation coefficients, using the equation $r^2 = (F/(F + \text{denominator d.f.}))$ (Rosenthal, 1991).

3. Results

We recorded 445 mammals belonging to 12 different species during the line transects, with the most abundant being fox with 147 records followed by wolf with 70 records and hare (*Lepus europaeus*) with 49 records (Appendix 1).

The total number of mammals recorded per transect ranged from 0 to 16, mean (SE) = 2.76 (0.22), median = 2, $N = 161$ transects. The number of predators per transect was 0–11, mean (SE) = 1.42 (0.12), median = 1, $N = 161$ transects. The number of prey per transect was 0–11, mean (SE) = 1.35 (0.15), median = 1, $N = 161$ transects. The level of radiation ranged from 0.01 to 225.00 μSv/h, mean (SE) = 5.52 μSv/h (0.61), median = 0.82 μSv/h, $N = 161$ transects. Thus, the level of radiation varied by a factor 22,500 among transects.

The abundance of mammals decreased with level of radiation, depended on species, and the effect of radiation varied among species as shown by the significant radiation by species interactions (Table 1). The largest negative effect was recorded for the fox (Pearson $r = -0.45$), while the weakest effect was recorded for the wolf ($r = +0.09$; see Appendix 1 for a list of effect sizes). A random effect model with site as a random factor showed that 44% of the variance occurred among sites. There was still a strong negative effect of radiation ($F_{1,94.52} = 25.46$, $P < 0.0001$, slope (SE) = −0.207 (0.041)), with a weak additional effect of coverage with shrub ($F_{1,151.2} = 4.53$, $P = 0.035$).

The total number of mammals per transect decreased significantly with level of radiation (Fig. 2), accounting for 31% of the variance in abundance. This model showed a good fit to the data ($F_{138,19} = 1.55$, $P = 0.14$).

The extent to which tracks represented the same individual should be reflected by time since last snowfall. A longer period since last snowfall should allow mammals to travel longer distances, and hence they should make more or repeated tracks in the snow. Indeed, there was a small, non-significant effect of time since last snowfall on recorded abundance of mammals despite the short time window used for the study (Table 2). The effect size of time since last snowfall was $r^2 = (F/(F + \text{denominator d.f.}))$ (Rosenthal, 1991) = 3.03/3.03 + 57.00 = 0.019, or a small effect. Therefore, we can conclude that this effect is not a major concern.

We made two additional analyses to validate our findings, First, if we reduced the 161 transects to the mean values for the 11 study areas shown in Fig. 1, we still find a strong negative relationship ($F_{1,9} = 5.81$, $r^2 = 0.39$, $P = 0.039$, estimate (SE) = −0.222 (0.092)). Indeed, the estimate (SE) in this conservative analysis did not differ significantly from that found when analyzing the 161 transects as statistically independent data points (−0.209 (0.025); Table 2).

Table 1
Abundance of mammals in relation to radiation, species and radiation by species interaction in 161 line transects around Chernobyl. The model had the statistics $F_{23,1908} = 22.69$, $r^2 = 0.21$, $P < 0.0001$.

Variable	Sum of squares	d.f.	*F*	*P*	Slope (SE)
Radiation (*R*)	0.833	1	48.24	<0.0001	−0.025 (0.004)
Species (*S*)	6.640	11	34.95	<0.0001	
$R \times S$	1.540	11	8.10	<0.0001	
Error	32.953	1908			

Table 2
Abundance of mammals in relation to radiation, habitat (coverage with shrub) and time since snowfall in 161 line transects around Chernobyl. The model had the statistics $F_{3,157} = 23.70$, $r^2 = 0.31$, $P < 0.0001$.

Variable	Sum of squares	d.f.	*F*	*P*	Slope (SE)
Radiation	4.229	1	69.62	<0.0001	−0.209 (0.025)
Shrub	0.455	1	7.50	0.0069	−0.176 (0.064)
Time since snowfall	0.184	1	3.03	0.084	−0.003 (0.002)
Error	9.536	157			

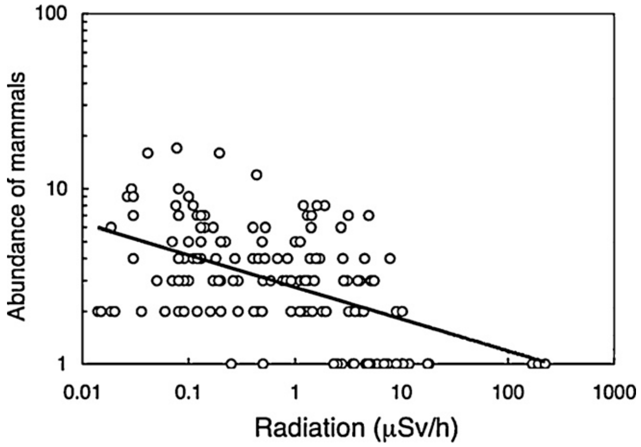

Fig. 2. Abundance of mammals in relation to background radiation level (μSv/h) according to line transects in areas around Chernobyl. The line is the linear regression line.

Second, if we nested background radiation within sites in a nested model we obtained a highly significant model that accounted for 60% of the variance (Table 3). The model showed a good fit to the data ($F_{105,34} = 1.32$, $P = 0.18$). There was a significant effect of site implying that the abundance of mammals differed among the 11 sites (Table 3). In addition, we found a significant effect of radiation nested within sites (Table 3). This implies that the abundance of mammals changed in response to changes in background radiation levels (Table 3). This effect of radiation on mammal abundance was statistically significant at the 0.01 level for four of the 11 study sites exceeding the null expectation of $0.01 \times 11 = 0.11$ significant effects by chance.

The abundance of predators was explained to 24% by abundance of prey, radiation and their interaction (Table 4). While the linear term for abundance of prey did not reach statistical significance, the abundance of predators increased with the squared abundance of prey, with an effect size of 0.23 (Table 4). In addition, there were fewer predators in areas with higher levels of radiation, with an effect size of 0.28 (Table 4). Finally, the number of predators increased disproportionately with the number of prey at high levels of radiation, as shown by the significant positive interaction that had an effect size of 0.18 (Table 4). The interaction between squared abundance of prey and radiation was not retained in the final model ($F_{1,154} = 0.04$, $P = 0.85$). Likewise, time since last snowfall was not retained in the model ($F_{1,154} = 0.57$, $P = 0.45$). A random effect model with site as a random factor showed that 44% of the variance occurred among sites. There was a strong negative effect of radiation ($F_{1,70.19} = 10.16$, $P = 0.0021$, slope (SE) = −0.122 (0.038)), a non-significant effect of number of prey ($F_{1,144} = 0.22$, $P = 0.64$) and a weak additional effect of number of prey squared ($F_{1,155.2} = 4.76$, $P = 0.031$, slope (SE) = 0.513 (0.235)). The number of prey by radiation interaction did not reach statistical significance ($F_{1,154.4} = 2.19$, $P = 0.14$).

Table 3
Abundance of mammals in relation to radiation nested within study sites around Chernobyl. The model had the statistics $F_{21,139} = 9.84$, $r^2 = 0.60$, $P < 0.0001$.

Variable	Sum of squares	d.f.	*F*	*P*
Radiation [site]	2.703	11	6.13	<0.0001
Site	4.548	10	4.55	<0.0001
Error	5.573	139		

4. Discussion

The main findings of this study of the abundance of mammal tracks in relation to level of radiation around Chernobyl were that (1) there were many more mammals in less contaminated areas independent of the statistical model, (2) species differed significantly in this response to radiation with some showing sharp decreases in abundance, while others did not, and (3) there was a functional response of predators to abundance of prey depending on level of radiation. These effects were demonstrated in generalized linear models, but also in random effect models with site as a random factor thereby controlling statistically for the potential non-independence of transects within sites.

The abundance of mammals around Chernobyl decreased with increasing level of background radiation, as revealed by the minimum number of individuals producing snow tracks along 100 m line transects. We also analyzed this relationship by conservatively reducing the entire dataset to mean values for the 11 study areas being separated by a maximum distance of 43 km although that did not change the conclusions. Likewise, a nested statistical model that considered the effects of radiation within sites also showed a negative effect of radiation on abundance. In this latter model the site variable will include variation among sites due to many different factors that were not considered explicitly in the study. Such reductions in abundance of animals in more contaminated areas have already been documented for birds, bumblebees, butterflies, dragonflies, grasshoppers and spiders (Møller and Mousseau, 2007a, 2009a). There was a significant interspecific difference in the response of mammals to radiation, with some species showing much stronger declines than others. The fox showed the strongest negative relationship between radiation and abundance, while the wolf had the weakest effect. We have

Table 4
Abundance of predators in relation to abundance of prey and time since snowfall in 161 line transects around Chernobyl. Time since snowfall and its interaction with abundance of prey and radiation were not retained in the model. The model had the statistics $F_{4,156} = 12.35$, $r^2 = 0.24$, $P < 0.0001$.

Variable	Sum of squares	d.f.	F	P	Slope (SE)
Abundance of prey (P)	0.058	1	1.33	0.25	0.084 (0.073)
Abundance of prey^2	0.398	1	9.07	0.0030	0.719 (0.239)
Radiation (R)	0.582	1	13.27	0.0004	−0.081 (0.022)
$P \times R$	0.216	1	4.93	0.028	0.187 (0.084)
Error	7.660	157			

previously demonstrated interspecific differences in relationship between radiation and abundance of birds (Møller and Mousseau, 2007b; Galván et al., 2011).

Line transects may have differed in efficiency among species. For example, mice and stoats (*Mustela erminea*) spend most of the time under the snow, making population density estimates based on snow tracks unreliable. Therefore, total abundance of mammals is clearly under-estimating the real abundance. We attempted to assess the reliability of our estimates of mammal abundance based on snow tracks by measuring the duration of time since last snowfall. We started conducting our line transects a few hours after snowfall ceased and we terminated transects during the following 1.5 days. Thus there was very limited time for accumulation of multiple tracks by the same individuals. We adopted two different methods for reducing this effect of accumulation. First, we only made very conservative estimates of the abundance of mammals by excluding any tracks that could possibly be attributed to more than the minimum possible number of individuals. Second, we estimated the time since last snowfall and included this variable in the analyses to account for accumulation of tracks over time. The effect of time since last snowfall was small, suggesting that this was not an important source of bias. Therefore, there is no reason to believe that the relative abundance of different mammal species in areas differing in level of radiation would be biased.

Predators are expected to track the populations of prey by showing numerical and functional responses. The Chernobyl situation is interesting from the perspective of interspecific interactions because the perturbation caused by radioactive contamination provides a semi-experimental situation where changes in the local abundance of prey is expected to lead to changes in the local abundance of predators. The shape of numerical and functional responses of predators can affect prey community stability and composition, with generalist predators either stabilizing (Erlinge et al., 1988; Henke and Bryant, 1999) or destabilizing the community (Bonsall and Hassell, 1997; Holt, 1977) depending on ecological conditions. We found evidence of the functional response of predators depending on the level of radiation. Predators were disproportionately common at high population densities of prey, and this effect of high densities of prey was particularly important at high levels of radiation. We suggest that high levels of radiation may render prey particularly susceptible to predation, through the effects of radiation on antioxidant levels, damage to DNA and other molecules or cyto-toxic effects of radiation. Finally, if the transect data provided biased estimates of abundance, there is no reason to expect positive associations between abundance of predators and abundance of prey. Thus, the evidence of a response by predators to the abundance of prey is consistent with our line transects capturing important biological information about the abundance of predators and prey.

In conclusion, we have shown that populations of mammals around Chernobyl have reduced abundance in the most contaminated areas independent of the statistical models, although this effect varies markedly among species. The abundance of predators was related to the level of radiation and prey abundance, with the effect of abundance of prey being particularly strong at high levels of radiation. Therefore, snow tracks provide a simple method for assessing the abundance of mammals in radioactively contaminated areas, but also for assessing the effects of background radiation on an interspecific interaction, predator–prey relationships under field conditions.

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