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REFERENCES

1. Thorup, K., Bisson, I.-A., Bowlin, M.S., Holland, R.A., Wingfield, J.C., Ramenofsky, M., and Wikelski, M. (2007). Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. *Proc. Natl. Acad. Sci. USA* 104, 18115–18119.
2. Chernetsov, N., Kishkinev, D., and Mouritsen, H. (2008). A long-distance avian migrant compensates for longitudinal displacement. *Curr. Biol.* 18, 188–190.
3. Gagliardo, A. (2013). Forty years of olfactory navigation in birds. *J. Exp. Biol.* 216, 2165–2171.
4. Kishkinev, D., Chernetsov, N., Heyers, D., and Mouritsen, H. (2013). Migratory reed warblers need intact trigeminal nerves to correct for a 1,000 km eastward displacement. *PLoS One* 8, e65847.
5. Kishkinev, D., Chernetsov, N., and Mouritsen, H. (2010). A double clock or jetlag mechanism is unlikely to be involved in detection of east-west displacements in a long-distance avian migrant. *Auk* 127, 773–780.
6. Zapka, M., Heyers, D., Hein, C. M., Engels, S., Schneider, N.-L., Hans, J., Weiler, S., Dreyer, D., Kishkinev, D., Wild, J. M., and Mouritsen, H. (2009). Visual but not trigeminal mediation of magnetic compass information in a migratory bird. *Nature* 461, 1274–1277.
7. Deutschlander, M.E., Phillips, J.B., and Munro, U. (2012). Age-dependent orientation to magnetically-simulated geographic displacements in migratory Australian silvereyes (*Zosterops l. lateralis*). *Wilson J. Ornithol.* 124, 467–477.
8. Heyers, D., Zapka, M., Hoffmeister, M., Wild J.M., and Mouritsen, H. (2010). Magnetic field changes activate the trigeminal brainstem complex in a migratory bird. *Proc. Natl. Acad. Sci. USA* 107, 9394–9399.
9. Boles, L.C., and Lohmann, K. (2003). True navigation and magnetic maps in spiny lobsters. *Nature* 421, 60–63.
10. Putman, N.F., Endres, C.S., Lohmann, C.M.F., and Lohmann, K.J. (2011). Longitude perception and bicoordinate magnetic maps in sea turtles. *Curr. Biol.* 21, 463–466.

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Long-term census data reveal abundant wildlife populations at Chernobyl

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Following the 1986 Chernobyl accident, 116,000 people were permanently evacuated from the 4,200 km² Chernobyl exclusion zone [1]. There is continuing scientific and public debate surrounding the fate of wildlife that remained in the abandoned area. Several previous studies of the Chernobyl exclusion zone (e.g. [2,3]) indicated major radiation effects and pronounced reductions in wildlife populations at dose rates well below those thought [4,5] to cause significant impacts. In contrast, our long-term empirical data showed no evidence of a negative influence of radiation on mammal abundance. Relative abundances of elk, roe deer, red deer and wild boar within the Chernobyl exclusion zone are similar to those in four (uncontaminated) nature reserves in the region and wolf abundance is more than 7 times higher. Additionally, our earlier helicopter survey data show rising trends in elk, roe deer and wild boar abundances from one to ten years post-accident. These results demonstrate for the first time that, regardless of potential radiation effects on individual animals, the Chernobyl exclusion zone supports an abundant mammal community after nearly three decades of chronic radiation exposures.

The Belarus sector of the Chernobyl exclusion zone, the Polesye State Radioecological Reserve (PSRER), covers 2,165 km², half of the total area, and has similar radiation levels to the Ukrainian sector (only ca. 1% of the Ukrainian sector is more contaminated). The PSRER provides a unique opportunity to test three key hypotheses concerning the resilience of wildlife to the world's worst nuclear accident.

Hypothesis 1 proposes that mammal abundances are negatively correlated with levels of radioactive contamination at Chernobyl. This hypothesis was not supported by the data. Mean number of tracks per 10 km (2008–2010) was assessed as a function of radiocaesium contamination density on 35 winter survey routes for elk, wolf (Figure 1), wild boar, roe deer, fox, and a combined category of other predatory and non-predatory mammals (see Figure S1 in the Supplemental Information published with this article online). Note that we used radiocaesium contamination density in statistical analyses; radiation dose rates are discussed in Supplemental Information.

For all species, our statistical models (which included habitat variation; see Supplemental Information) rejected radioactive contamination as an important predictor of mammal density within the PSRER. Although census data do not give direct information on population metrics such as reproductive success or longevity, a scenario in which depressed populations in the highly contaminated areas are supported (on a daily basis) by rapid influx and habitat utilization from less contaminated areas seems highly unlikely. Home ranges of the species examined [6] give length scales smaller than, or of the same order as, route length.

A study of small mammals by Baker *et al.* [7] also found no evidence of population declines at Chernobyl. However, a previous study of mammals using track counts [3] reported a negative relationship between radiation levels and mammal density. The discrepancy with our data is likely because this previous study [3] covered only 16.1 km of transects examined just once. Our data are derived from transects with a total length that is 20 times larger and repeated in two (21 routes) or three (14 routes) years.

Hypothesis 2 proposes that densities of large mammals are suppressed at PSRER (Chernobyl zone) compared with those in four uncontaminated nature reserves in Belarus. Again, we found that this hypothesis was not supported by the empirical data. We analysed population density estimates (2005–2010) derived from winter track survey routes and published by the Belarus Ministry of Natural Resources [8]. Similar densities of large ungulates (hoofed mammals) were

observed at PSRER for elk, red deer, roe deer and wild boar compared with four uncontaminated reserves in Belarus (Figure S2). Wolf density at PSRER was seven times higher. Though there is uncertainty in estimating population density from winter track survey data, our comparison of *relative* density between reserves is robust because the same census methods were used in each reserve.

The rejection of this second hypothesis is supported by comparing track counts at PSRER with the Bryansky Forest reserve [9] in Russia, 250 km away. Elk and boar counts (from 2008–2010) were broadly similar in the two reserves (ratio PSRER:Bryansky = 1.30:1 for elk, 0.66:1 for boar). Wolf and lynx tracks were respectively 19 and 1.3 times higher, but roe deer four times lower, at PSRER.

Interpretation of this comparison of ungulate densities among reserves is difficult owing to the much higher wolf densities but lower human pressure at PSRER compared with other reserves (Supplemental Information). Nonetheless, the data indicate that mammal densities at PSRER are not atypical of what would be expected in an uncontaminated nature reserve in the region. Due to natural variation in mammal densities and habitats, this comparative analysis cannot exclude some impact of radiation on populations at PSRER, though we found no evidence of this in our data that refuted Hypothesis 1.

Our data also did not support Hypothesis 3, which proposed that densities of large mammals declined in the period between 1 and 10 years after the accident. Aerial survey counts of wild boar (1987–1996), elk and roe deer (1988–1996) increased significantly ($p < 0.01$) over time (Figure 1). For boar, the significance of this decreased when we excluded two years with lower survey coverage (Supplemental Information). Increases in large non-predatory mammals from 1987–1996 were accompanied by a large increase in wolves, a likely cause of the decline in wild boar (a primary prey of wolves in the PSRER) from 1993–1994 (Figure 1), although an outbreak of African swine fever also contributed to this decline. Before the Chernobyl accident, mammal population densities were likely

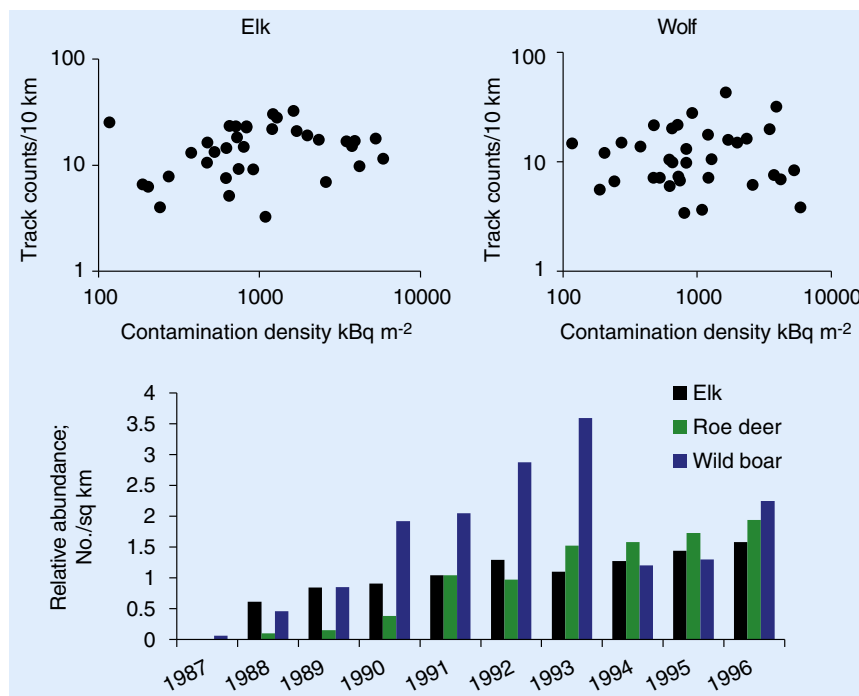


Figure 1. Animal abundances in the Chernobyl exclusion zone.

(Top) Mean number of track counts per 10 km (in 2008–2010) for elk and wolf plotted against mean ^{137}Cs contamination density of each route. Analysis using linear mixed models including habitat variables found no evidence of correlation between mammal density and contamination density. See Supplemental Information for other species studied. (Bottom) Change in relative abundance of three species in the 10 years after the Chernobyl accident.

depressed due to hunting, forestry and agriculture.

Extremely high dose rates during the first six months after the accident significantly affected animal health and reproduction at Chernobyl [1]. However, any potential long-term radiation damage to populations is not apparent from our trend analysis of large mammal abundances. Increases in elk and wild boar populations in the Chernobyl exclusion zone occurred at a time (early 1990s) when these species were undergoing a rapid decline in former Soviet Union countries owing to major socio-economic changes (which resulted in increased rural poverty and weakened wildlife management) [10]. Our data on time trends cannot separate likely positive effects of human abandonment of the Chernobyl exclusion zone from a potential negative effect of radiation (though we could detect no such negative effect in our test of Hypothesis 1). Nevertheless, they represent unique evidence of wildlife's resilience in the face of chronic radiation stress.

None of our three hypotheses postulating radiation damage to large

mammal populations at Chernobyl were supported by the empirical evidence. The results from these unique data will help society balance the negative impacts to wildlife from chronic radiation exposures against how “the removal of humans alleviates one of the more persistent and ever growing stresses experienced by natural ecosystems” [1].

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures and additional analyses, as well as two figures and three tables can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.08.017>.

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REFERENCES

1. IAEA (2006). Environmental Consequences of the Chernobyl Accident and their Remediation: Twenty Years of Experience (Vienna: International Atomic Energy Agency).
2. Möller, A.P., and Mousseau, T.A. (2009). Reduced abundance of insects and spiders linked to radiation at Chernobyl 20 years after the accident. *Biol. Lett.* 5, 356–359.
3. Möller, A.P., and Mousseau, T.A. (2013). Assessing effects of radiation on abundance of mammals and predator–prey interactions in Chernobyl using tracks in the snow. *Ecol. Indic.* 26, 112–116.
4. UNSCEAR (1996). Sources and Effects of Ionizing Radiation; Report to the General Assembly with Scientific Annex (Vienna: United Nations).
5. Garnier-Laplace, J., Della-Vedova, C., Gilbin, R., Copplestone, D., Hingston, J., and Ciffroy, P. (2006). First derivation of predicted-no-effect values for freshwater and terrestrial ecosystems exposed to radioactive substances. *Environ. Sci. Tech.* 40, 6498–6505.
6. Lindstedt, S.L., Miller, B.J., and Buskirk, S.W. (1986). Home range, time, and body size in mammals. *Ecol.* 67, 413–418.
7. Baker, R.J., Hamilton, M.J., Van Den Bussche, R.A., Wiggins, L.E., Sugg, D.W., Smith, M.H., Lomakin, M.D., Gaschak, S.P., Bundova, E.G., and Rudenskaya, G.A. (1996). Small mammals from the most radioactive sites near the Chernobyl nuclear power plant. *J. Mammal.* 77, 155–170.
8. Ministry of Natural Resources (2011). National system of environmental monitoring of the Republic of Belarus: results of observations: 2010 (Minsk: Belarusian Research Centre “Ecology”).
9. Sitnikov, E.F. (2013). Bryansky Forest: The study of natural processes occurring in nature and connections between different parts of the ecosystem, volume 2 (Ministry of Natural Resources of Russia).
10. Bragina, E.V., Ives, A.R., Pidgeon, A.M., Kuemmerle, T., Baskin, L.M., Gubar, Y.P., Piquer-Rodríguez, M., Keuler, N.S., Petrosyan, V.G., and Radeloff, V.C. (2015). Rapid declines of large mammal populations after the collapse of the Soviet Union. *Conserv. Biol.* 29, 844–853.

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