

Cite as: V. Kubelka *et al.*, *Science*
10.1126/science.aaw9893 (2019).

Response to Comment on “Global pattern of nest predation is disrupted by climate change in shorebirds”

Vojtěch Kubelka^{1,2,3*}, Miroslav Šálek⁴, Pavel Tomkovich⁵, Zsolt Végvári⁶, Robert P. Freckleton⁷, Tamás Székely^{1,2,8*}

¹Department of Evolutionary Zoology and Human Biology, University of Debrecen, H-4032 Debrecen, Hungary. ²Milner Centre for Evolution, University of Bath, Claverton Down, Bath BA2 7AY, UK. ³Department of Biodiversity Research, Global Change Research Institute, Czech Academy of Sciences, 603 00 Brno, Czech Republic. ⁴Faculty of Environmental Sciences, Czech University of Life Sciences, 165 21 Prague, Czech Republic. ⁵Zoological Museum, Moscow MV Lomonosov State University, Moscow 125009, Russia. ⁶MTA Centre for Ecological Research, Danube Research Institute, 1113 Budapest, Hungary. ⁷Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK. ⁸State Key Laboratory of Biocontrol and College of Ecology and Evolution, Sun Yat-sen University, Guangzhou 510275, China.

*Corresponding author. Email: kubelkav@gmail.com (V.K.); t.szekely@bath.ac.uk (T.S.).

Bulla *et al.* dispute our main conclusion that the global pattern of nest predation is disrupted in shorebirds. We disagree with Bulla *et al.*'s conclusions and contest the robustness of their outcomes. We reaffirm our results that provide clear evidence that nest predation has increased significantly in shorebirds, especially in the Arctic.

In our study (*1*) we showed significant increases in daily nest predation rate in ground-nesting shorebirds that were especially strong in the Arctic. Bulla *et al.* (*2*) raise four concerns about our findings. Here, we highlight statistical and methodological problems in Bulla *et al.*'s analyses.

First, Bulla *et al.* argue that we should have presented evidence of a statistically significant interaction between region/latitude and year/period on daily nest predation rate in order to demonstrate that the temporal trend of increasing predation rate varies spatially. This criticism ignores that the analyses both we and they reported are based on a logarithmically transformed response variable [$\log(x + 0.01)$: transformation applied based on model diagnostics]. The presence or absence of interactions based on transformed data is difficult to interpret. For example, log-transformation means that on the arithmetic scale, the effects of model predictors are multiplicative, which implies interactive effects.

This issue is demonstrated in Fig. 1. The data suggest strong temporal increases in daily nest predation (Fig. 1A) (*3*) with an evident difference in responses between the Northern and Southern Hemispheres. The lines in Fig. 1 are based on a model fitted to the log-transformed data and confirm the presence of both temporal and geographic effects. Diagnostic analysis confirms that the geographic difference is clearly evident in the data, becoming larger through time (Fig. 1B). The simple model reported in Fig. 1A captures this increase, despite the lack of an interaction term, because of the data transformation. However, Bulla *et al.* failed to recognize this and were therefore unable to de-

tect the patterns shown in Fig. 1.

Figure 1C shows an example of the complexity underneath this overall global pattern: Differences between the Arctic and the nearest region (North temperate) are small on average, but recently daily nest predation has risen notably in the Arctic (Fig. 1D). Our published analyses and visualizations were designed to explore the nature of such interactions by examining the spatiotemporal patterns in more detail. Figures 2 and 3 in (*1*) demonstrate these spatially variable effects on which our conclusions are based and include mean trends with associated confidence intervals.

Second, Bulla *et al.* suggest that our models were pseudo-replicated, although they acknowledge that we corrected for spatial autocorrelation. In our spatial models (*1*, *4–6*), spatial dependency is modeled as a random variance in which all points from the same location have the same (maximal) covariance. Our spatial term also accounts for possible covariance between sites that are close to each other, which the models of Bulla *et al.* do not (*7*).

Third, Bulla *et al.* raised concerns about “observation time” (which they refer to as *B*). *B* represents the proportion of incubation and egg-laying periods for which successful nests in a particular population are followed by researchers. These values are used to estimate nest exposure using Beintema’s method (*8*); this converts “apparent predation” to daily nest predation values. Alternatively, if the exposure and number of depredated nests are given, then daily nest predation may be computed directly (*1*, *9*, *10*). Bulla *et al.* argue that the increase in daily nest predation over time

may be an artifact of using Beintema's methodology (8). We do not agree with Bulla *et al.* for three reasons:

1) For 56 populations where data using both approaches were available, the estimated values were not statistically different from the directly computed ones [see supplementary material of (1) and Fig. 2A]. The only trend suggested is a slight but nonsignificant underestimation of daily nest predation using Beintema's conversion after year 2000 (Fig. 2B) that is opposite to the concern raised by Bulla *et al.*

2) The simulations performed by Bulla *et al.* include observation times (B) from 0.1 to 0.9 [figure 1H in (2)] with the artifactual increases in predation rate for historic data when B is very low (0.1 to 0.5). However, B should in principle vary from 0.5 of the incubation and egg-laying period in studies with random nest search to approximately 0.9 when all nests are found during the egg-laying period as a result of intensive research (8, 11). Bulla *et al.* computed an average $B = 0.65$ for more than 10,000 shorebird nests at 16 Arctic sites and do not report $B < 0.5$ at any site or in any population (12). Lower values ($B < 0.5$) might be plausible only in exceptional circumstances (e.g., when low nest search intensity is restricted to the late breeding period only). However, no estimate of B in our dataset was lower than 0.5 (1, 13); therefore, Bulla *et al.*'s simulations using $B < 0.5$ for our data are unjustified.

3) Contrary to Bulla *et al.*, we find that the global temporal increase in nest predation is significant when daily nest predation was either calculated directly or converted from "apparent predation" [table S3 in (1); Fig. 2C] (14).

Finally, Bulla *et al.* hypothesize that increased research intensity over the years could have influenced the temporal increase in nest predation. To address this issue, we scored the research intensity for the data used in (1); however, we found no evidence that intensive research may have elevated nest predation rates (Fig. 2D). Therefore, notwithstanding the possible negative effect of disturbance through more intensive study, it is unlikely that research intensity would have contributed to the temporal increase in nest predation we reported (1).

Taken together, these findings provide further evidence that the global pattern of nest predation was disrupted in shorebirds, and this conclusion remains unaffected by the concerns raised by Bulla *et al.* (2). The key results of (1) are straightforward, supported by simple models and data: There is a strong temporal increase in nest predation rates at a global scale, with significant spatial variation. Our conclusions are reinforced by a detailed study of five shorebird species that reported increased nest predation for all five species between 1948 and 2006, using 200 data points from six European countries (15). Our results remain robust, and together they appear to reveal a significant, previously underappreciated global threat to shorebirds.

REFERENCES AND NOTES

1. V. Kubelka, M. Šálek, P. Tomkovich, Z. Végvári, R. P. Freckleton, T. Székely, Global pattern of nest predation is disrupted by climate change in shorebirds. *Science* **362**, 680–683 (2018). doi:10.1126/science.aat8695 Medline
2. M. Bulla *et al.*, Comment on "Global pattern of nest predation is disrupted by climate change in shorebirds". *Science* **364**, eaaw8529 (2019). doi:10.1126/science.aaw8529
3. V. Kubelka *et al.*, Data, R codes, and supporting information for Response to Comment on "Global pattern of nest predation is disrupted by climate change in shorebirds". Open Science Framework, <https://osf.io/46bt3/>.
4. W. Jetz, R. P. Freckleton, Towards a general framework for predicting threat status of data-deficient species from phylogenetic, spatial and environmental information. *Philos. Trans. R. Soc. B* **370**, 20140016 (2015). doi:10.1098/rstb.2014.0016 Medline
5. R. P. Freckleton, W. Jetz, Space versus phylogeny: Disentangling phylogenetic and spatial signals in comparative data. *Proc. R. Soc. B* **276**, 21–30 (2009). doi:10.1098/rspb.2008.0905 Medline
6. V. Kubelka *et al.*, Data and R codes from "Global pattern of nest predation is disrupted by climate change in shorebirds". Dryad (2018). doi:10.5061/dryad.45g90h4.
7. The large number of random group levels (111 species and 152 localities) used by Bulla *et al.*, relative to the number of observations (237), as well as the large proportion of groups represented by just single observations (59 of 111 species and 114 of 152 localities), raise concerns about the robustness of their approach—specifically, the identifiability of the random and residual terms when the fixed effects vary at the level of localities.
8. A. J. Beintema, Inferring nest success from old records. *Ibis* **138**, 568–570 (1996). doi:10.1111/j.1474-919X.1996.tb08084.x
9. H. Mayfield, Nesting success calculated from exposure. *Wilson Bull.* **73**, 255–261 (1961).
10. H. F. Mayfield, Suggestions for calculating nest success. *Wilson Bull.* **87**, 456–466 (1975).
11. Observation time (B) varying between 0.52 and 0.67 for six Dutch shorebird species can be derived from Beintema's work (5). $B > 0.5$ was found for all investigated shorebirds, including cryptic common snipe (*Gallinago gallinago*), which is well known for the difficulty of nest finding.
12. M. Bulla, J. Reneerkens, E. L. Weiser, R. B. Lanctôt, B. Kempenaers, Supporting information for Comment on "Global pattern of nest predation is disrupted by climate change in shorebirds." Open Science Framework, <https://osf.io/x8fs6/>.
13. Bulla *et al.*'s claim that "for 38% of the 128 populations where Kubelka *et al.* used $B > 0.5$, we found no information in the reference to suggest that this was appropriate" is not substantiated in their comment; see information on data collection and research intensity in relevant source publications referenced in (1).
14. Bulla *et al.*'s treatment of random effects, as we note earlier, is problematic because of the preponderance of groups represented by single observations: When we removed groups represented by single observations and reran the analysis [figure 1F in (2)], the temporal trend was indeed statistically significant using the approach of Bulla *et al.* (3).
15. M. Roodbergen, B. van der Werf, H. Hötter, Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: Review and meta-analysis. *J. Ornithol.* **153**, 53–74 (2012). doi:10.1007/s10336-011-0733-y

ACKNOWLEDGMENTS

We thank the people who provided us with unpublished data or additional information to already published articles or helped us with gray literature and useful contacts; see (1) for details. D. Childs and A. J. Beintema helped us with their critical comments on the issues discussed within the article. **Funding:** Supported by ÉLVONAL-KKP 126949 of the Hungarian government (V.K. and T.S.); Ministry of

Education, Youth and Sports of the Czech Republic grant LO1415 (V.K.); Ministry of Education, Youth and Sports of the Czech Republic, Kontakt II LH13278 (M.Š.); MSU Zoological Museum grant AAAA-A16-116021660077-3 (P.T.); and Royal Society Wolfson Merit Award and grant NKFIH-2558-1/2015 (T.S.). **Author contributions:** All authors conceived the study; V.K. collected the data with help from all co-authors; and V.K., R.P.F., and T.S. analyzed the data and wrote the paper with input from all co-authors. **Competing interests:** The authors declare that they have no competing interests.

9 March 2019; accepted 29 May 2019

Published online 14 June 2019

10.1126/science.aaw9893

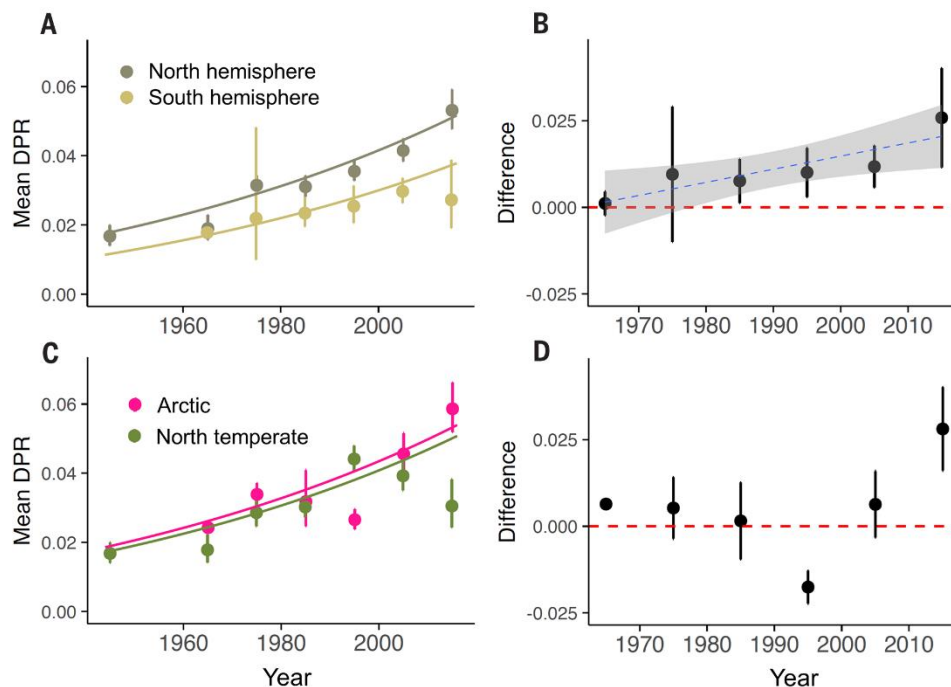


Fig. 1. Temporal and spatial variation in daily nest predation rate (DPR) at a global scale. We fitted the simplest model [$\log(\text{DPR} + 0.01)$ as a linear function of latitude and year]; both latitude and year are highly statistically significant. This is a simpler model than any used by Bulla *et al.* (2), but notably has a lower Akaike information criterion (AIC) than the models they considered. Note that although the model does not include an interaction term on the log scale, the lines diverge on the arithmetic scale, indicating geographically divergent outcomes. This applies equally to the models of Bulla *et al.* We also provide comparison with raw data as decadal averages (\pm SEM) in all graphs; see (3) for model details. (A) Fitted values (lines) for Northern and Southern Hemispheres compared with data. (B) Difference of DPR in the Northern relative to the Southern Hemisphere; the blue dashed line with 95% confidence intervals indicates a significant increase in this difference over the period of study. (C) Comparison of Arctic and North temperate regions. (D) Difference of DPR in the Arctic relative to the North temperate region. See (1) for details and sample sizes.

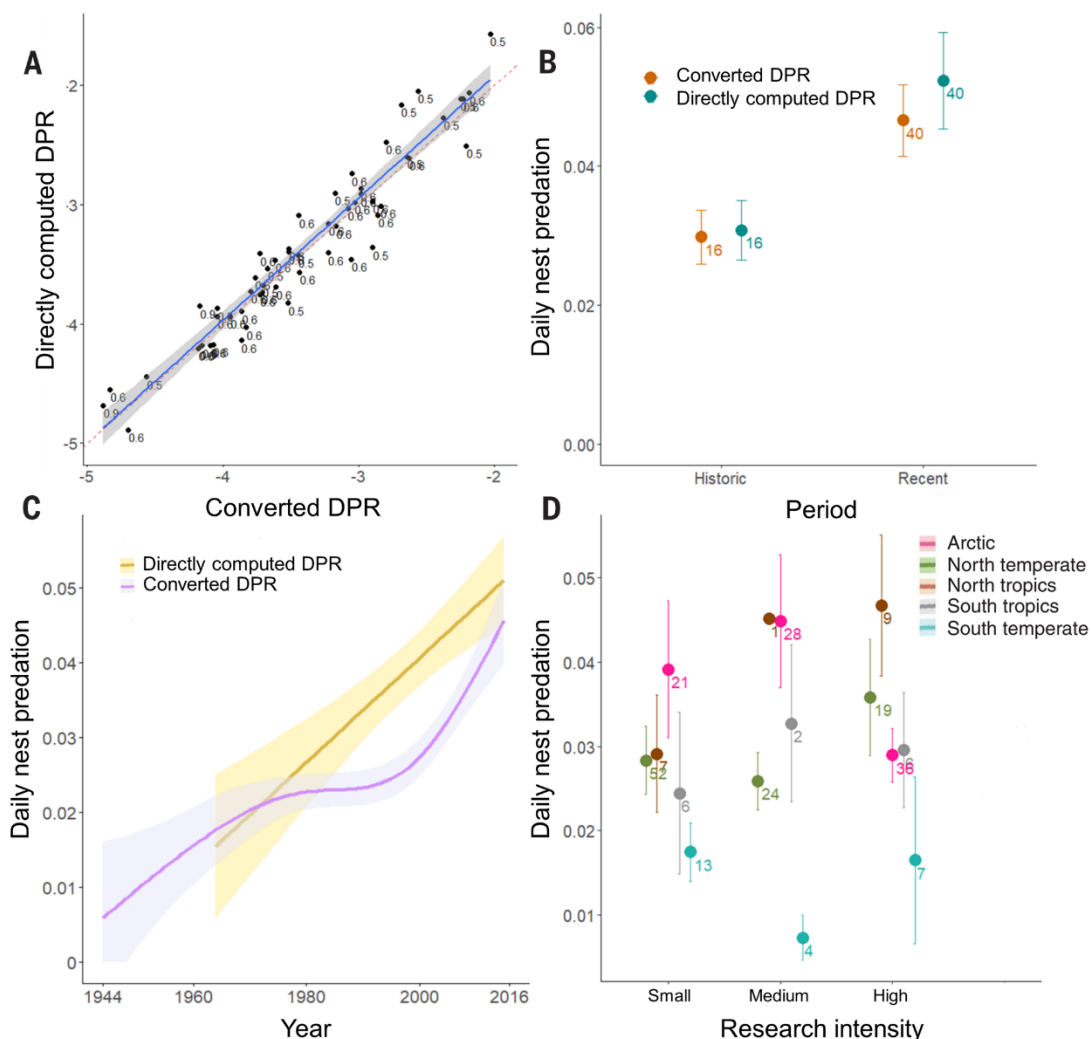


Fig. 2. Variation in DPR in relation to computation method and research intensity. (A) Correlation between directly calculated DPR and DPR values using Beintema's conversion (5). The relationship (\pm confidence interval) is in blue, the red dashed line represents parity, and observation time (*B*) is noted next to each data point. (B) Directly calculated and converted DPR in historic (before 2000) and recent (after 2000) periods. Data in (A) and (B) represent 56 populations; see (1) for details. (C) Temporal trend in directly calculated DPR (97 populations) and converted DPR (140 populations). Generalized additive model fits with 95% confidence intervals are shown; see table S3 in (1) for model description. (D) Daily nest predation variation according to research intensity: Small = infrequent visits to nests (e.g., to measure eggs); Medium = repeated nest visits to deploy nest-monitoring devices (e.g., trail cameras) near nest and/or adult trapping at a few nests; High = trapping and banding of breeding adults on a majority of nests. [Nonsignificant effect of research intensity on DPR: estimate = 0.115, SEM = 0.106, $z = 1.09$, $P = 0.280$; linear mixed-effects kinship model with control for phylogeny (species level of phylogeny + random effect of the species), spatial autocorrelation and number of nests per population.] Data are means \pm SEM for five latitudinal areas separately; see (1, 3) for details. Number of populations is given next to the relevant data points in (B) and (D).



Response to Comment on “Global pattern of nest predation is disrupted by climate change in shorebirds”

Vojtěch Kubelka, Miroslav Šálek, Pavel Tomkovich, Zsolt Végvári, Robert P. Freckleton, and Tamás Székely

Science **364** (6445), eaaw9893. DOI: 10.1126/science.aaw9893

View the article online

<https://www.science.org/doi/10.1126/science.aaw9893>

Permissions

<https://www.science.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of service](#)

Science (ISSN 1095-9203) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.

Copyright © 2019, American Association for the Advancement of Science