



The effect of climate change on avian offspring production: A global meta-analysis

Lucyna Halupka^{a,1} , Debora Arlt^{b,c} , Jere Tolvanen^d , Alexandre Millon^{e,f} , Pierre Bize^g , Peter Adamík^{h,i} , Pascal Albert^j, Wayne J. Arendt^k , Alexander V. Artemyev^l , Vittorio Baglione^m , Jerzy Bańburaⁿ , Mirosława Bańbura^o, Emilio Barba^p , Robert T. Barrett^q, Peter H. Becker^r , Eugen Belski^s , Mark Bolton^t, E. Keith Bowers^u , Joël Bried^{v,w} , Lyanne Brouwer^{x,y} , Monika Bukacińska^z , Dariusz Bukaciński^{aa} , Lesley Bulluck^{ab}, Kate F. Carstens^{ac} , Inês Catry^{ad,ae} , Motti Charter^{af} , Anna Chernomoretz^{ag} , Rita Covas^{ah,ai,aj} , Monika Czuchra^{ak} , Donald C. Dearborn^{al,am} , Florentino de Lope^{an} , Adrián S. Di Giacomo^{ao}, Valery C. Dombrovski^{ap} , Hugh Drummond^{aq} , Michael J. Dunn^{ar} , Tapio Eeva^{as} , Louise M. Emmerson^{at} , Yngve Espmark^{au} , Juan A. Fargallo^{av} , Sergey I. Gashkov^{aw} , Elena Yu. Golubova^{ax} , Michael Griesser^{ay,az} , Michael P. Harris^{ba} , Jeffrey P. Hoover^{bb} , Zuzanna Jagiełło^{bc} , Patrik Karell^{bd,be} , Janusz Kloskowski^{bf} , Walter D. Koenig^{bg,bh} , Heikki Kolonen^{bi} , Małgorzata Korczak-Abshire^{bj} , Erkki Korpimäki^{bk} , Indrikis Krams^{bl,bm,bn} , Miloš Krist^{bo} , Sonja C. Krüger^{bp} , Boris D. Kuranov^{bq} , Xavier Lambin^{br} , Michael P. Lombardo^{bs} , Andrey Lyakhov^{bt} , Alfonso Marzá^{bu} , Anders P. Møller^{bv} , Verónica C. Neves^{bw} , Jan Tøttrup Nielsen^{bx} , Alexander Numerov^{by} , Beata Orłowska^{bz} , Daniel Oro^{ca} , Markus Öst^{cb,cc,cd} , Richard A. Phillips^{ce} , Hannu Pietiäinen^{cf} , Vicente Polo^{cg} , Jiří Porkert^{ch} , Jaime Potti^{ci} , Hannu Pöysä^{cj} , Thierry Printemps^{ck} , Jouke Prop^{cl} , Petra Quillfeldt^{cm} , Jaime A. Ramos^{cn} , Pierre-Alain Ravussin^{co} , Robert N. Rosenfield^{cp} , Alexandre Roulin^{cq} , Dustin R. Rubenstein^{cr} , Irina E. Samusenko^{cs} , Denis A. Saunders^{ct} , Michael Schaub^{cu,cd,ce} , Juan C. Senar^{cf} , Fabrizio Sergio^{cg} , Tapio Solonen^{ch} , Diana V. Solovyeva^{ci} , Janusz Stępniewski^{ck,kl} , Paul M. Thompson^{cl} , Marcin Tobolka^{cm,nn} , János Török^{co,nn,oo} , Martijn van de Pol^{cp,pp,qq} , Louis Vernooij^{pr} , Marcel E. Visser^{ps} , David F. Westneat^{pt} , Nathaniel T. Wheelwright^{qu} , Jarosław Wiącek^{qv} , Karen L. Wiebe^{uw} , Andrew G. Wood^{vn} , Andrzej Wuczyński^{ww} , Dariusz Wysocki^{wx} , Markéta Zárybnická^{xx} , Antoni Margalida^{yy,zz}, and Konrad Halupka^{aa}

Edited by Nils Stenseth, University of Oslo, Oslo, Norway; received September 9, 2022; accepted March 22, 2023

Climate change affects timing of reproduction in many bird species, but few studies have investigated its influence on annual reproductive output. Here, we assess changes in the annual production of young by female breeders in 201 populations of 104 bird species (N = 745,962 clutches) covering all continents between 1970 and 2019. Overall, average offspring production has declined in recent decades, but considerable differences were found among species and populations. A total of 56.7% of populations showed a declining trend in offspring production (significant in 17.4%), whereas 43.3% exhibited an increase (significant in 10.4%). The results show that climatic changes affect offspring production through compounded effects on ecological and life history traits of species. Migratory and larger-bodied species experienced reduced offspring production with increasing temperatures during the chick-rearing period, whereas smaller-bodied, sedentary species tended to produce more offspring. Likewise, multi-brooded species showed increased breeding success with increasing temperatures, whereas rising temperatures were unrelated to reproductive success in single-brooded species. Our study suggests that rapid declines in size of bird populations reported by many studies from different parts of the world are driven only to a small degree by changes in the production of young.

climate change | birds | offspring production | meta-analysis

Global temperatures have been rising significantly during the 20th and 21st centuries (1). Higher temperatures and changes in precipitation patterns have resulted in shifts of climatic zones, altering the conditions that animals experience on their breeding grounds, their wintering grounds, and during migration (2). Such climate changes have multiple effects on populations of diverse organisms, including birds (3, 4).

Most studies analyzing the effects of climate change on birds have focused on changes in timing of migration and breeding. In many cases, these studies have found that migratory species arrive earlier on their breeding grounds, and that many birds start to lay their eggs earlier in the season in response to higher temperatures (4–6). This is not surprising given that many species of birds exhibit phenotypic plasticity and breed earlier during warm springs (7, 8).

Less well explored, and more difficult to predict, are consequences of climate-driven advancements in laying dates (9, 10). In particular, few studies have investigated the production of offspring in avian populations in relation to climate change. Work that has been conducted indicates that responses vary enormously. Some show advanced laying dates, but other breeding parameters, including offspring production, are unchanged (8, 11). Other studies have found a decline in the production of young (10, 12). Such a decline may be a result of mismatch between time of peak food availability and time of maximum energetic requirements of the offspring (13, 14), but also more frequent adverse

Significance

Numerous studies have shown that climate change has altered avian timing of breeding. However, little is known about climate-driven changes in offspring production. We collected long-term breeding data on 201 populations of 104 bird species (N = 745,962 clutches) from all continents, between 1970 and 2019, to assess temporal changes in annual offspring production by female breeders in relation to changes in local temperatures and species' life history traits. Overall, offspring production declined over time, but responses of different populations to rising temperatures were diverse. Our analyses suggest that negative effects of rising temperatures on offspring production will mainly affect migratory and larger-bodied species, whereas smaller-bodied sedentary species may benefit from warmer climate.

¹To whom correspondence may be addressed. Email: lucyna.halupka@uwr.edu.pl.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2208389120/-/DCSupplemental>.

Published May 1, 2023.

weather and weather extremes (10, 15, 16), higher predation (17, 18), or a decline in food (19). However, it is also possible that some species may benefit from breeding earlier as temperatures increase. Several studies have found increased fledgling production in warmer breeding seasons (20–22), or after warm winters (23).

We used a meta-analysis to assess changes in offspring production in avian populations worldwide over the last 50 y (Fig. 1 and *SI Appendix, Table S1*), a period over which global temperatures have risen by about 1 °C (1). We controlled for possible effects of phylogeny (24), life history of a species (9), migratory habits (25), latitude (26), direct human impacts (27), and changes in local temperature and precipitation as components of climate (15, 20). Our analyses complement prior studies that have investigated climate-driven changes in timing of egg-laying and related breeding parameters (26, 28, 29).

Based on earlier research (28, 30), we hypothesized that multi-brooded species would increase the annual number of fledged young, because they are able to take advantage of protracted food resource availability (13), whereas single-brooded species would fledge fewer young per year, because they may have problems synchronizing timing of breeding with peak food availability (12, 25). Because larger-bodied species usually adapt more slowly to environmental changes due to their slower “pace of life” (31), we anticipated that declining trends in annual offspring production would be observed more often in larger-bodied than in smaller-bodied species. Finally, we predicted that declines in offspring production would be observed less often in sedentary species than in migrants, because the latter are more likely to be constrained in their phenological response to climate change (32, 33).

Results

Overall Trends. Changes in offspring production were normally distributed and varied between -0.171 and 0.196 SDs per year from the long-term averages (Fig. 2). The funnel plot was symmetrical (Kendall’s rank test: $\tau = 0.002$, $P = 0.97$), and trim-and-fill analysis indicated no directional bias in the sample of studies included in the analyses.

In 114 of 201 (56.7%) populations, offspring production decreased over time; 17.4% of these did so significantly. Conversely, in 87 populations (43.3%), offspring production increased over time, 10.4% significantly. The grand effect size was slightly, but significantly, less than zero, suggesting an overall reduction in offspring production (Table 1). An analysis of spatial autocorrelation of population effect sizes yielded a Moran I of -0.003 (95% bootstrap percentile interval:

-0.110 to 0.107), which was close to the value of -0.005 expected under the null hypothesis of no effect, indicating that directional changes in offspring production were not spatially clustered across geographical regions. The analyses of other life history and demographic traits indicated that nest success decreased and egg-laying started progressively earlier. Changes in clutch size and changes in duration of egg-laying periods were nonsignificant (Table 1).

Correlates of Offspring Production. We conducted univariate meta-regressions to assess the effects of life history and ecological characteristics of populations and their environments on changes in annual offspring production (Fig. 3). Changes in offspring production were positively associated with changes in clutch size and nest success. We also found a negative relationship between temporal changes in offspring production and body mass, with relatively larger species performing worse. None of the remaining life history traits produced a significant beta coefficient. The effect of nesting in nest-boxes was marginally positively significant. Ecological factors, including absolute latitude, environment type, protection status of the study area, and a Human Footprint Index (HFI), were not associated with changes in offspring production. Similarly, long-term trends in temperature and precipitation at different periods of the breeding season did not explain variation in changes in offspring production. In particular, changes in offspring production in relation to changing rainfall were consistently negligible.

Interactive Effects on Offspring Production and Nest Success.

In the next step, we used multivariate generalized linear mixed models (GLMMs) to model changes in offspring production and its two proxies: changes in clutch size and changes in nest success. In all models, we used the same sets of random effects (population, species, and phylogeny), and fixed predictor variables: log body mass, number of broods in a breeding season, migratory habits, and temporal change in local ambient temperatures. We considered two types of models: one that included all possible interactions between predictors and a simpler model including only two-way interactions of change in ambient temperature with the remaining fixed factors. For rate of change in local ambient temperature, we sequentially substituted measures taken in five phenological periods (enumerated in Fig. 3). Models were compared using Akaike’s information criterion (AIC) (*SI Appendix, Table S2*). Models with only two-way interactions outperformed the model with all possible interactions. With respect to temperatures, temperature trends in the nestling period produced the best model of changes in offspring production. Temperature trends in the prelaying period

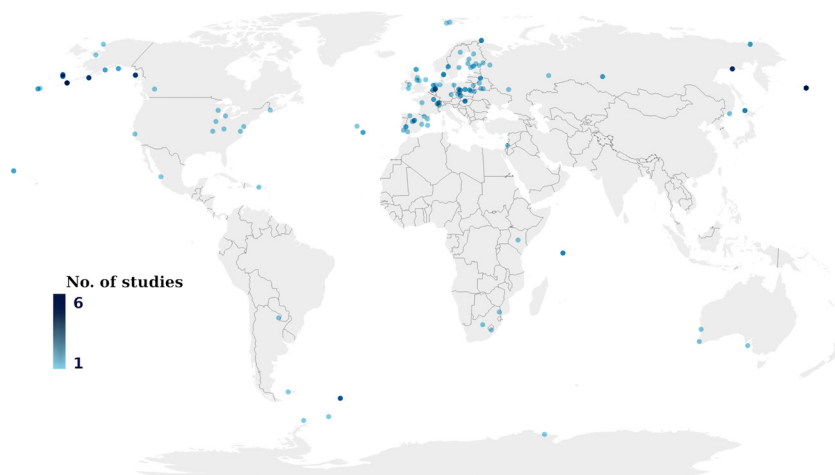


Fig. 1. Distribution of sampling study areas around the world. Overlapping study areas result in darker dots.

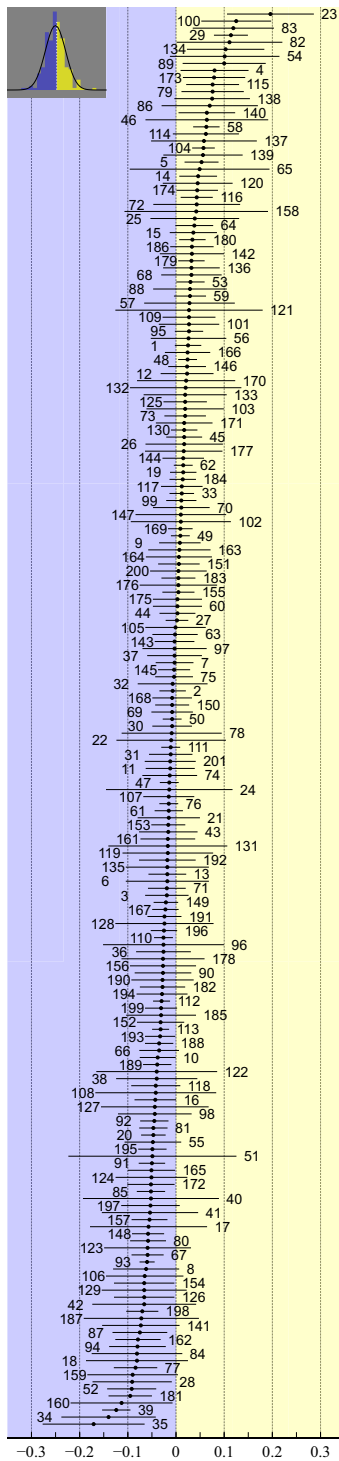


Fig. 2. Change ($\pm 95\%$ confidence limits) in mean number of offspring per female, measured in SD per year, in 201 populations of 104 species. Results were ranked from most negative to most positive. Numbers on the graph refer to population identifiers in *SI Appendix, Table S1*. The inset shows the frequency distribution of the effect sizes with a normal curve overlay.

yielded the best model of changes in nest success, and temperature trends in laying period yielded the best model of changes in clutch size. Raw data and interactions between predictors in the model of changes in offspring production and model of changes in nest success are visualized in Fig. 4.

The final model of changes in offspring production (left section of Table 2 and Fig. 4B) revealed that increasing ambient temperatures during the chick-rearing period were associated with

Table 1. Phylogenetically corrected grand effect sizes and their 95% bootstrap percentile confidence intervals of annual changes in demographic and life history traits of bird species around the world over the period 1970 to 2019

Trait	Grand ES	95% c.i.
Changes in offspring production (SDs), N = 104 species	-0.012	-0.019, -0.005
Changes in clutch size (SDs), N = 63	0.006	-0.001, 0.012
Changes in nest success (%p), N = 100	-0.026	-0.054, -0.008
Changes in date of first egg (days), N = 104	-0.066	-0.093, -0.039
Changes in duration of laying period (days), N = 104	0.009	-0.058, 0.066

Grand effect sizes with 95% confidence intervals not covering a value of zero are in bold.

increased offspring production in small and/or sedentary birds, whereas most migratory birds (except for the smallest ones) experienced declines in offspring production in warming climates. Increasing offspring production tended to correlate with nesting in nest-boxes (Fig. 3). Therefore, we added nest-boxes as a fixed factor to test its effect in combination with other predictors. It was insignificant ($\beta = -0.003$, 95% c.i.: -0.022 to 0.016), and the resulting model (*SI Appendix, Table S3*) had $\Delta AIC = 6.2$, indicating a poorer fit.

The final model of changes in nest success (middle section of Table 2 and Fig. 4C) suggested that the proportion of fledged nests declined in larger-bodied species. In single-brooded species, nest success was independent of climate changes. In multi-brooded bird species, nest success improved with increasing temperatures.

The final model of changes in clutch size (right section of Table 2) did not include significant interactions between predictor variables. The only important predictor was body mass, with large species producing smaller clutches.

The results of a sensitivity analysis (bar graphs in Fig. 4) showed that body mass alone captured around 40% of the uncertainty in trends of offspring production and nest success. Body mass also explained 60% of the uncertainty in the model of changes in clutch size. The other predictors had minor first-order effects. In particular, first-order sensitivity indices of changes in local temperatures were negligibly small in all final models. However, coupled effects of climate variability and life history traits were influential.

Discussion

Our meta-analysis shows that overall production of young in bird populations has been declining over the past 50 y across the globe and across species. This effect is significant even though it appears small: The decline is about 0.01 standard deviations per year in long-term mean offspring production. Over the course of decades, however, this can lead to a large reduction in the number of produced young. We also found substantial differences among sampled populations: 56.7% showed a declining trend in offspring production, and 43.3% of populations tended to produce more offspring. Generally, bird species whose offspring production declined were relatively large and migratory, whereas species whose production increased were small bodied and sedentary. This is a rough generalization, as some species do not fit this pattern. Additionally, in 5 of 35 species (14.3%) represented by more than one population, we found significant, but opposite trends in offspring production. This large variation suggests that reasons for changes in offspring

Predictor [No. species, populations]

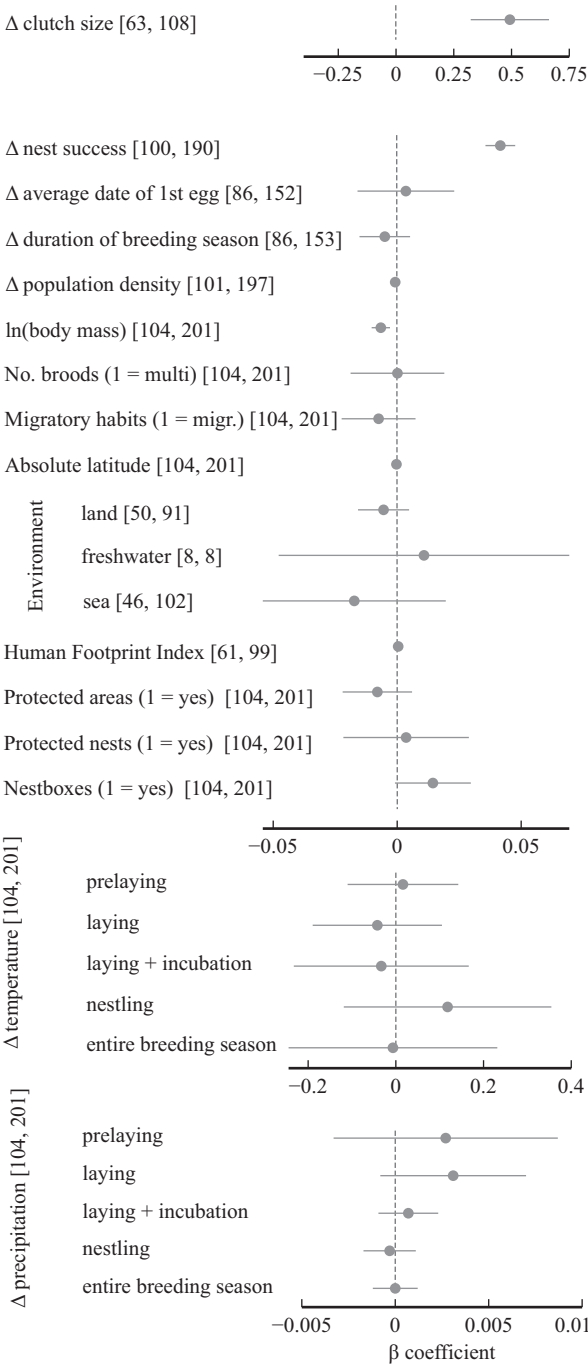


Fig. 3. Beta coefficients ($\pm 95\%$ confidence limits) of univariate meta-regressions in which standardized change in mean annual number of offspring per female was predicted by life history, demographic, ecological, and climatic variables. In all models, phylogenetic correlations along with identifiers of populations and species were included as random effects. Predictors expressed as a rate of change per year are shown as Δ . Note the different scales on each part of the plot.

production reflect, at least to some extent, some differences in local conditions. However, the change in offspring production was not associated with protection status of study areas or with anthropogenic transformation of their habitats.

Body mass, both as a stand-alone predictor and in relation to climate change, was the most important correlate of temporal changes in clutch size and offspring production. Our model suggests that larger species are more vulnerable to declines in offspring production and nest success (Fig. 4A), and that body mass exceeding

1 kg for sedentary species, and 50 g for migratory species, is associated with negative trends in offspring production for climate warming at a rate of 0.1°C per year (Fig. 4B). Larger-bodied species may be slower in responding to changing environmental and climatic conditions due to their lower fecundity, extended maturation, and longer generation time (34, 35). Recent analyses suggest that selection favoring smaller body size under warming condition operates at the within-species, as well as among-species, level (36).

Sensitivity analysis of the final models indicates that climate change does not correlate with avian offspring production directly, but through complex interactions with their life history and ecological traits. Thus, climate variability is an influential factor when coupled with migratory habits and number of broods raised in the breeding season.

Our results suggest that nonmigratory species, especially smaller ones, are usually able to adjust to changes in local conditions and may benefit from climate warming (20, 37, 38), whereas migratory species, with the exception of the smallest, may suffer (25). This corroborates the phenology-mismatch hypothesis, which proposes that a lack of correlation between rate of warming in breeding and wintering areas causes a phenological mismatch on breeding grounds, resulting in population declines (32).

Previous research has provided evidence that an increase in local temperatures (both mean temperatures and extremes) may be correlated with changes in nest success (16, 17, 20, 22), a pattern found only for multi-brooded species in our analysis (Fig. 4C). As we did not have information on causes of nest losses, we cannot assess whether this reflects changes in predation pressure or some other factor. Multi-brooded birds often experience selection pressure for early breeding (39). A warming climate may be beneficial for such species, because earlier development of vegetation allows for better nest concealment, thereby reducing the risk of nest depredation and/or resulting in more food at the beginning of the season (13, 22). Nevertheless, nest-site selection may involve trade-offs between reduced risk of detection versus enhanced escape opportunities and information about approaching predators (40), which may result in selection for intermediate nest concealment (41, 42).

Several recent studies have provided evidence that populations of birds are severely declining on different continents (43–45). However, we found a relatively small overall decline in offspring production of avian populations across the globe. This suggests that recent population declines may reflect changes in adult and juvenile survival (10, 43, 46), and, to a lesser degree, changes in offspring production. It is also possible that habitat loss and deteriorating conditions make a higher proportion of the total population of declining bird species unable to breed, a hypothesis that remains to be tested.

Our dataset was biased in terms of the geographic location of populations, as we collected few data from the tropics and central parts of continents. Tropical regions host a large proportion of avian diversity and are experiencing rapid anthropogenic change, whereas areas inside continents usually undergo stronger climatic changes than areas affected by marine conditions (1). We therefore expect that the heterogeneity in our sample may be lower than the true global heterogeneity.

In conclusion, analyses based on 201 wild bird populations from all continents reveal that offspring production has declined during recent decades, but with considerable variation among species and populations. Species with relatively large body mass are the most vulnerable to decline in offspring production. Climate change appears to influence changes in offspring production through complex interactions with ecological and life history traits of species. Future studies should identify the reasons for nest failures to understand better the factors underlying declines in offspring production in avian populations.

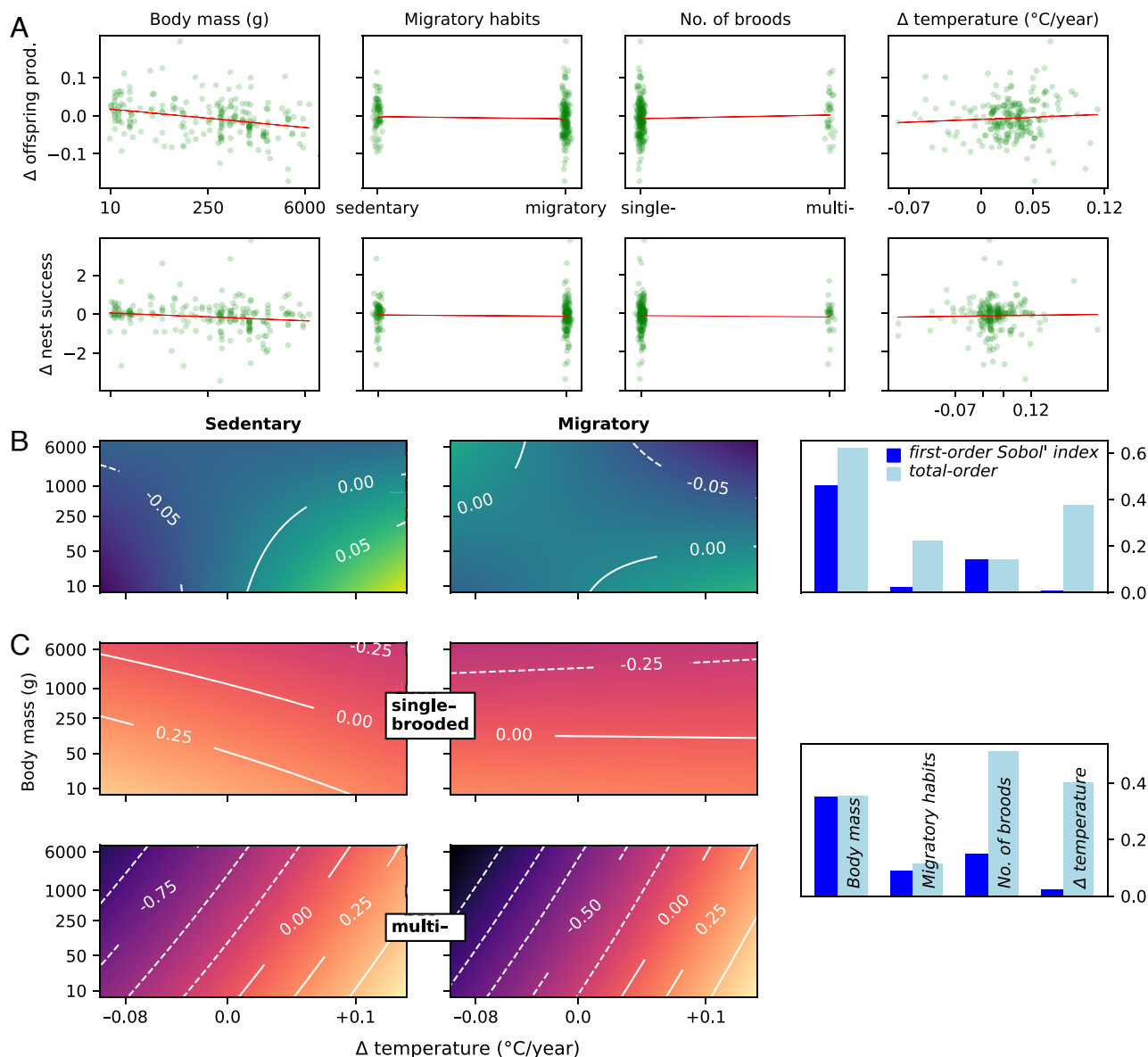


Fig. 4. Trends in offspring production and nest success. Some redundant axis labels have been pruned to reduce visual clutter. (A) Raw data of change in the number of offspring female⁻¹ season⁻¹ in standard deviations per year and change in nest success (percentage points per year) regressed on life history traits and changes in local temperatures. Temperatures refer to the nestling period (upper plot) and prelaying period (lower plot). (B) Heatmaps visualizing the interactive effect of body mass and changes in local temperatures on the predicted change in mean number of offspring per female, expressed in SD per year, and represented by contours and colors. The bar graphs show the results of a sensitivity analysis. (C) Heatmap of predicted change in nest success, expressed in percentage points per year, with the results of a sensitivity analysis. The models in B and C are described in Table 2.

Materials and Methods

Definitions. We defined offspring production as mean annual number of fledglings produced by a breeding female in a population monitored throughout the breeding season. Mean clutch size was calculated for all clutches (first, replacements and second clutches) laid by females. We defined nest success as the proportion of successful clutches (producing at least one fledgling) out of all clutches monitored across a breeding season. Second broods were defined as those initiated after successfully fledging young from a first clutch. We classified a species' population as single-brooded or multi-brooded depending on the presence and frequency of second broods in a population (SI Appendix, Table S1 and SI Text S1). We created three environmental categories, dividing species into land birds (not associated with water), freshwater species (breeding and foraging in inland water bodies), and seabirds. For each study population, we also calculated the temporal trend in the number of breeding females present at a study area. We divided study sites into protected and nonprotected; if >50% of a study area was under some forms of legal protection (national parks, nature reserves, etc.), we classified it as protected, otherwise as nonprotected.

Similarly, we divided studies with nests protected against predators and nests nonprotected; if >50% of nests were protected (e.g., concrete nest-boxes, fences around nests), we classified the population as nest-protected. Finally, we divided studies into those using nest-boxes (if >50% of clutches were laid in nest-boxes) and those using natural nest sites (monitoring open-nesting and cavity-nesting species).

Criteria for Data Inclusion. The criteria for a dataset to be included in our project were: 1) a minimum study period of 15 y, during which data were collected for at least 10 breeding seasons; 2) average seasonal number of breeding females was greater than 10; 3) in multi-brooded species, females were individually marked; and 4) research had to be conducted for the whole breeding season to determine accurately the fate of successive broods, and annual offspring production of each breeding female.

Data Collection. Data were obtained from two major sources: 1) published information and 2) unpublished data from authors conducting long-term studies on the breeding biology of single species. 1) To locate information published in the current

Table 2. Final meta-regression models of annual changes in fitness-related traits

Term	Changes in offspring production [104, 201]		Changes in nest success [100, 190]		Changes in clutch size [63, 108]	
	Estimate	95% c. l.	Estimate	95% c. l.	Estimate	95% c. l.
Intercept	0.002	−0.043, 0.047	0.567	0.130, 1.003	0.065	0.015, 0.115
Ln (body mass)	−0.003	−0.009, 0.003	−0.080	−0.139, −0.020	−0.011	−0.017, −0.004
Migratory habits (sedentary vs. migratory)	0.012	−0.010, 0.034	−0.191	−0.374, −0.009	−0.019	−0.045, 0.007
Number of broods (single- vs. multi-brooded)	−0.021	−0.055, 0.014	−0.457	−0.695, −0.219	0.001	−0.031, 0.033
Change in temperature*	1.260	0.254, 2.267	−1.768	−7.110, 3.574	−0.348	−0.981, 0.285
Ln(body mass) × change in temp.	−0.139	−0.271, −0.007	0.078	−0.749, 0.905	0.037	−0.051, 0.125
Migratory habits × change in temp.	−0.620	−1.174, −0.066	1.363	−1.226, 3.951	0.324	−0.101, 0.749
Number of broods × change in temp.	0.006	−0.727, 0.739	7.381	3.069, 11.693	−0.340	−0.828, 0.149

In all models, phylogenetic correlations between species and identifiers of populations and species were included as random effects. Beta coefficients whose 95% confidence limits do not include zero are shown in bold. The number of species and populations is in square brackets. Models of changes in offspring production and nesting success are visualized in Fig. 4. *At the laying period in the model of clutch size, prelaying period in the model of nest success, and nestling period in the model of offspring production.

century concerning long-term changes in offspring production of avian populations, we undertook an exhaustive literature search in Google Scholar using the following key words: breeding, nesting, breeding success, offspring production, population productivity, climate change, and laying dates. Because we wanted to use standardized estimates of changes in offspring production across time (see below), we looked for publications that included original data. From published literature, we collected data on 72 bird populations representing 28 species (SI Appendix, SI Text S2). 2) Our literature search enabled us to identify researchers who potentially had long-term data on annual production of young in the bird populations they studied. Between October 2018 and April 2019, we contacted 313 authors of long-term studies asking them whether they would like to collaborate in our meta-analysis project. A total of 101 authors shared their data on 86 species and 129 populations (for details on searching process, see SI Appendix, SI Text S3). From both data sources, we collected a total of 201 datasets on 104 bird species (for problems with species number, see SI Appendix, SI Text S4) covering the histories of 745,962 clutches. The data were gathered in both hemispheres between 1970 and 2019 (Fig. 1), and different populations were sampled over a period ranging from 15 to 49 breeding seasons (median 26; interquartile range 20 to 35) (SI Appendix, Table S1). Literature sources, including descriptions of field methods used in the studies included in the analyses, can be found in SI Appendix, Table S4.

In addition to the data on offspring production, we collected data on laying dates, clutch size, nest success, breeding density, and proportion of females with second broods or replacement clutches. These data were not provided by all researchers, and not found in all literature sources.

Meteorological, Body Mass, and Migratory Data. Meteorological data for the study areas, including mean monthly temperatures and total monthly precipitation, were provided by authors or, for published data, obtained from the National Oceanic and Atmospheric Administration (<http://www.ncdc.noaa.gov/cdo-web/datatools/findstation>) or Tutiempo.net (<https://en.tutiempo.net/climate/europe.html>). We used data from meteorological stations closest to study areas with complete records across study years. For each area, we calculated mean temperatures (°C) and total precipitation (mm) corresponding with each of the five breeding periods: 1) prelaying (a month preceding commencement of egg laying); 2) egg laying; 3) egg laying and incubation; 4) nestling period; and 5) whole breeding season (from the commencement of egg laying until the end of parental care). The information about timing and duration of these periods was obtained from main investigators or extracted from the literature (47, 48). We subsequently calculated the rate of change in mean temperature and total precipitation over the study period using linear regressions as an index of climate change intensity.

Data on mean female body mass for each species were obtained from *Handbook of Avian Body Masses* (49). The distribution of body masses was strongly skewed; therefore, we ln-transformed it for our analyses. Migratory status (full migrant vs. sedentary/partial migrant) followed the International Union for Conservation of Nature classification (50).

HFI. For each study area, we calculated a Human Footprint Index (HFI), which quantifies the degree to which humans have impacted the landscape (on 1 km² grid cells) by combining measures of human population density, buildings, crop land, pasture land, night-time lights, railways, roads, and navigable waterways (27). Values of the index range from 0 to 50. HFI data were extracted from ref. 51 using QGIS software (version 3.22.11). For each study area, we calculated a mean HFI score by overlaying the HFI raster layer with a site raster layer. Because HFI data are not available for islands, we were able to calculate the index for only 114 continental bird populations.

Statistical Analysis. Analyses were conducted using R version 4.2.2 (52) and Phylometa version 1.3 (53). They were carried out in two steps: 1) we estimated grand effect sizes for a group of variables describing changes in species' parameters and 2) using metaregression, we looked for factors explaining heterogeneity in effect sizes (hereafter ESs) from the first step.

A list of all variables used in the analysis (including the species' parameters) is provided in SI Appendix, Table S5. All ESs studied were slopes of linear regressions, in which response variables were regressed on time (years). Slopes are intuitively interpreted as changes per annum. Annual production of offspring per female and clutch size were standardized and expressed as the number of standard deviations from the long-term mean measured across all study years of a particular population. This allowed comparison across species whose mean offspring production and clutch sizes differed.

Because of between-study heterogeneity due to variation in local environmental conditions, life histories of study species, and research methods, we used random-effects models in all meta-analyses. Sensitivity of the model due to publication bias was assessed using funnel plots and a trim-and-fill method (54).

We controlled for a potential bias due to phylogenetic relatedness among species (SI Appendix, Table S1 and SI Text S4) using a set of 5,000 equally plausible trees, downloaded from birdtree.org (55, 56). Grand ESs of changes in species' parameters were calculated by an iterative procedure with original phylogenetic trees. For meta-regression modeling, we built a 50% majority-rule consensus tree (56) using the R package "ape," version 5.5 (57).

Grand ESs in Table 1 were calculated using Phylometa software. We reran 5,000 iterations, each time using a different phylogenetic tree, and a subset of

ESs in question, which included only a single record for each species. If a species was represented by several local populations, one was selected at random for each iteration. Grand ESs were means across all resamples, with 95% confidence limits represented by the 2.5th and 97.5th percentiles.

Meta-regression models (Fig. 3, Table 2, and Fig. 4) were run using R package "metafor", version 3.4 (54). Each model included the same set of random effects: species and study identification (to control for nonindependence of multiple studies of the same species) and species identity associated with phylogenetic correlations (to control for nonindependence due to common ancestry).

In analyses where changes in offspring production and nest success were regressed upon different sets of climate variables, we used Akaike's information criterion to assess the performance of competing models (58) (*SI Appendix, Table S2*) and to select climate variables for final meta-regression models (Table 2).

For sensitivity analysis of the final models, we used Sobol's global variance decomposition method (59) implemented in R package "sensobol" version 1.1.3 (60). This procedure decomposes variance into fractions (Sobol's indices), which isolate effects of predictor variables and their interactions. Pseudo-random samples for the model's predictions were generated using a Latin hypercube sampling design. Estimates of Sobol's indices were based on Azzini's algorithm, using 10,000 bootstrap iterations, which guaranteed convergence under the criterion that the 95% confidence interval around the most sensitive predictor was less than 5% of its sensitivity index. For each predictor variable, we reported first-order and total-order indices. The former measures the fraction of the output variance explained by a respective predictor alone, whereas the latter includes effects of its interactions with other predictors.

Data, Materials, and Software Availability. All data and R scripts relevant to the article are available at Figshare (61). Other study data are included in the article and/or *SI Appendix, Tables S1–S3*.

ACKNOWLEDGMENTS. We are grateful to our collaborators who worked with us and collected field data. The list of principal collaborators and institutions is published in *SI Appendix, Table S6*. We thank Heather Renner for the information about the data collected by Alaska Maritime National Wildlife Refuge. We sincerely appreciate valuable comments and suggestions made by two reviewers, which helped us in improving the manuscript. This meta-analysis was financed by the grant of the Polish National Science Centre (Narodowe Centrum Nauki) (no. 2017/27/B/NZ8/00465) awarded to Lucyna Halupka.

Author affiliations: ^aOrnithological Station, Faculty of Biological Sciences, University of Wrocław, Wrocław 50-335, Poland; ^bDepartment of Ecology, Swedish University of Agricultural Sciences, Uppsala SE-750 07, Sweden; ^cSLU Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala SE-750 07, Sweden; ^dDepartment of Ecology and Genetics, University of Oulu, Oulu 90014, Finland; ^eAix Marseille University, University of Avignon, Centre National de la Recherche Scientifique (CNRS), Institut de Recherche pour le Développement (IRD), Institut Méditerranéen Biodiversité & Ecologie (IMBE), Aix-en-Provence 13545, France; ^fGroupe d'Etudes et de Protection des Busards (GepB), Beuvry 52110, France; ^gSwiss Ornithological Institute, Sempach CH-6204, Switzerland; ^hDepartment of Zoology, Faculty of Science, Palacký University, Olomouc 771 46, Czech Republic; ⁱMuseum of Natural History, Olomouc 771 73, Czech Republic; ^jPrivate address, Cormost 10800, France; ^kUSDA Forest Service, International Institute of Tropical Forestry, Sabana Field Research Station, Luquillo 00773, PR; ^lDepartment of Zoology, Institute of Biology, Karelian Research Center, Russian Academy of Sciences, Petrozavodsk 185910, Russia; ^mDepartamento de Biodiversidad y Gestión Ambiental, Universidad de León, León 24071, Spain; ⁿDepartment of Experimental Zoology and Evolutionary Biology, Faculty of Biology, University of Łódź, Łódź 90-237, Poland; ^oCavanilles' Institute of Biodiversity and Evolutionary Biology, University of Valencia, Valencia E46080, Spain; ^pDepartment of Natural Sciences, Tromsø University Museum, Tromsø NO-9037, Norway; ^qInstitute of Avian Research "Vogelwarte Helgoland", head office Wilhelmshaven, Wilhelmshaven 26386, Germany; ^rInstitute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg 620144, Russia; ^sCentre for Conservation Science, Royal Society for the Protection of Birds, Aberdeen AB10 1YP, UK; ^tDepartment of Biological Sciences, Edward J. Meeman Biological Station, and Center for Biodiversity Research, University of Memphis, Memphis TN 38152; ^uInstitute of Marine Sciences - OKEANOS, University of the Azores, Horta 9901-862, Portugal; ^vPrivate address, 64200 Biarritz, France; ^wDepartment of Zoology & Ecology, College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia; ^xDivision of Ecology & Evolution Research, School of Biology, The Australian National University, Canberra, ACT 2601, Australia; ^yDepartment of Environmental Conservation, Institute of Biological Sciences, Cardinal Stefan Wyszyński University of Warsaw, Warsaw 01-938, Poland; ^zDepartment of Biology and Center for Environmental Studies, Virginia Commonwealth University, Richmond, VA 23284; ^{aa}FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa; ^{ab}Research Centre in Biodiversity and Genetic Resources (CIBIO) / Research Network in Biodiversity and Evolutionary Biology (InBIO), Laboratório Associado, Universidade do Porto, Vairão 4485-601, Portugal; ^{ac}Research Centre in Biodiversity and Genetic Resources (CIBIO) / Research Network in Biodiversity and Evolutionary Biology (InBIO), Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, Lisbon 1349-017, Portugal;

^{ad}BIOPOLIS Program in Genomics, Biodiversity and Land Planning, Research Centre in Biodiversity and Genetic Resources (CIBIO), Vairão 4485-661, Portugal; ^{ae}Shamir Research Institute and Department of Geography and Environmental Studies, University of Haifa, Haifa 3498838, Israel; ^{af}Laboratory of Ornithology, Scientific and Practical Center for Biological Resources of National Academy of Sciences of Belarus, Minsk 220072, Belarus; ^{ag}Department of Behavioural Ecology, Faculty of Biological Sciences, University of Wrocław, Wrocław 50-335, Poland; ^{ah}Biology Department, Bates College, Lewiston, ME 04240; ^{ai}Division of Organisms and Environment, School of Biosciences, Cardiff University, Cardiff CF10 3AX, UK; ^{aj}Department of Anatomy, Cellular Biology and Zoology, University of Extremadura, Badajoz E-506071, Spain; ^{ak}Laboratorio de Biología de la Conservación, Centro de Ecología Aplicada del Litoral, Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET), Corrientes 3400, Argentina; ^{al}Laboratory of Molecular Zoology, National Academy of Sciences, Minsk 220072, Belarus; ^{am}Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad de México 04510, Mexico; ^{an}British Antarctic Survey, Natural Environment Research Council, Cambridge CB3 0ET, UK; ^{ao}Department of Biology, University of Turku, Turku 20014, Finland; ^{ap}Australian Antarctic Division, Department of Agriculture, Water and the Environment, 7050 Kingston TAS, Australia; ^{aq}Department of Biology, Norwegian University of Science and Technology, Trondheim 7491, Norway; ^{ar}Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas (CSIC), Madrid 28006, Spain; ^{as}Department of Museum Technologies, Zoology Museum, Tomsk State University, Tomsk 634050, Russia; ^{at}Institute of Biological Problems of the North, Far Eastern Branch, Russian Academy of Sciences, Magadan 685000, Russia; ^{au}Department of Biology, University of Konstanz, Konstanz 78457, Germany; ^{av}Center for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz 78457, Germany; ^{aw}Department of Collective Behavior, Max Planck Institute of Animal Behavior, Konstanz 78457, Germany; ^{ax}UK Centre for Ecology & Hydrology, Penicuik EH26 0QB, UK; ^{ay}Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Urbana-Champaign, IL 61820; ^{az}Institute of Zoology, Poznań University of Life Sciences, Poznań 60-625, Poland; ^{baa}Bioeconomy Research Team, Novia University of Applied Sciences, Raseborg FI-10600, Finland; ^{bab}Evolutionary Ecology Unit, Department of Biology, Lund University, Lund SE-223 62, Sweden; ^{bac}Hastings Reservation, University of California Berkeley, Carmel Valley, CA 93924; ^{bad}Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850; ^{bae}Private address, FI-14870 Tuulos, Finland; ^{bae}Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Warsaw 02-106, Poland; ^{bae}Department of Zoology and Animal Ecology, Faculty of Biology, University of Latvia, Riga 1004, Latvia; ^{bah}Department of Biotechnology, Daugavpils University, Daugavpils 5401, Latvia; ^{bai}Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Tartu 51010, Estonia; ^{baa}Conservation Services Division, Ezemvelo KwaZulu-Natal Wildlife, Cascades 3202, South Africa; ^{baa}School of Life Sciences, Centre for Functional Biodiversity University of KwaZulu-Natal, Pietermaritzburg 3201, South Africa; ^{baa}Department of Vertebrate Zoology and Ecology, Tomsk State University, Tomsk 634050, Russia; ^{baa}School of Biological Sciences, University of Aberdeen, Aberdeen AB24 2TZ, UK; ^{baa}Biology Department, Grand Valley State University, Allendale, MI 49401-9403; ^{baa}Ecologie Systématique Evolution, Centre National de la Recherche Scientifique (CNRS), Université Paris-Saclay, Gif-sur-Yvette 91190, France; ^{baa}Private address, 9870 Sindal, Denmark; ^{baa}Department of Zoology and Parasitology, Voronezh State University, Voronezh 394006, Russia; ^{baa}Theoretical and Computation Ecology Lab, Centre d'Estudis Acañats de Blanes (CEAB), Consejo Superior de Investigaciones Científicas, Blanes 17300, Spain; ^{baa}Environmental and Marine Biology, Abo Akademi University, Turku 20500, Finland; ^{baa}Novia University of Applied Sciences, Raseborg FI-10600, Finland; ^{baa}Department of Biosciences, University of Helsinki, Helsinki FI-00014, Finland; ^{baa}Department of Biology and Geology, Universidad Rey Juan Carlos, Móstoles 28933, Spain; ^{baa}Hradec Králové 500 02, Czech Republic; ^{baa}Estación Biológica de Doñana - CSIC, Consejo Superior de Investigaciones Científicas (CSIC), Seville 41092, Spain; ^{baa}Department of Environmental and Biological Sciences, University of Eastern Finland, Joensuu FI-80101, Finland; ^{baa}Arctic Centre, University of Groningen, Groningen 9718CW, the Netherlands; ^{baa}Department of Animal Ecology and Systematics, Justus Liebig University, Giessen 35392, Germany; ^{baa}Department of Life Sciences, Marine and Environmental Sciences Centre (MARE), University of Coimbra, Coimbra 3000-456, Portugal; ^{baa}Private address, CH-1446 Baulmes, Switzerland; ^{baa}Department of Biology, University of Wisconsin-Stevens Point, Stevens Point, WI 54481; ^{baa}Department of Ecology and Evolution, University of Lausanne, Lausanne CH-1015, Switzerland; ^{baa}Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027; ^{baa}Weetangera, Australian Capital Territory 2614, Australia; ^{baa}Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Bern CH-3012, Switzerland; ^{baa}Department de Vertebrats, Museu de Ciències Naturals de Barcelona, Barcelona 08003, Spain; ^{baa}Luontotutkimus Solonen Oy, Helsinki FI-00960, Finland; ^{baa}Panurus Monitoringi Inwentaryzacje Opinie Przyrodnicze, Osieczna 64-113, Poland; ^{baa}School of Biological Sciences, Lighthouse Field Station, University of Aberdeen, Cromarty IV11 8YL, UK; ^{baa}Konrad Lorenz Institute of Ethology, University of Veterinary Medicine, Vienna 1160, Austria; ^{baa}Department of Systematic Zoology and Ecology, Behavioural Ecology Group, ELTE Eötvös Loránd University, Budapest H-1117, Hungary; ^{baa}Integrative Ecology Research Group, Eötvös Loránd Research Network - Eötvös Loránd University - The Hungarian Natural History Museum, Budapest H-1117, Hungary; ^{baa}Department of Animal Ecology, Netherlands Institute of Ecology, Wageningen 6708PB, the Netherlands; ^{baa}Department of Physical Sciences, College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia; ^{baa}Department of Biology, University of Kentucky, Lexington, KY 40506-0225; ^{baa}Department of Biology, Bowdoin College, Brunswick, ME 04011; ^{baa}Department of Zoology and Nature Protection, Institute of Biological Sciences, Maria Curie-Skłodowska University, Lublin 20-033, Poland; ^{baa}Department of Biology, University of Saskatchewan, Saskatoon S7N 5E2, Canada; ^{baa}Institute of Nature Conservation, Polish Academy of Sciences, Kraków 31-120, Poland; ^{baa}Department of Vertebrate Zoology and Anthropology, Szczecin University, Szczecin 71-415, Poland; ^{baa}Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Prague 16521, Czech Republic; ^{baa}Institute for Game and Wildlife Research, IREC (CSIC-UCLM-JCCM), Ciudad Real E- 13005, Spain; and ^{baa}Pyrenean Institute of Ecology, Consejo Superior de Investigaciones Científicas (CSIC), Jaca 22700, Spain

Author contributions: L.H. and K.H. designed research; L.H. and M. Czuchra conducted literature search and collected meteorological data; L.H., P. Adamik, P. Albert, W.J.A., D.A., A.V.A., V.B., J. Bañbura, M. Bañbura, E. Barba, R.T.B., P.H.B., E. Belskii, P. B., M. Bolton, E.K.B., J. Bried, L. Brouwer, M. Bukacińska, D.B., L. Bulluk, J.F.C., I.C., M. Charter, A.C. R.C., D.C.D., F.d.L., A.S.D.G., V.C.D., H.D., M.J.D., T.E., L.M.E., Y.O.E., J.A.C., S.I.G., E.Y.G., M.G., M.P.H., J.P.H.,

P.K., J.K., W.D.K., H.K., M.K.-A., E.K., I.K., M.K., S.K., B.D.K., X.L., M.P.L., A.L., A. Margalida, A. Marzal, A. Millon, A.P.M., V.C.N., J.T.N., A.N., B.O., D.O., M.Ö., R.A.P., H. Pietiäinen, V.P., J. Porkert, J. Potti, H. Pöysä, T.P., J. Prop, P.Q., J.A.R., P.-A.R., R.N.R., A.R., D.R.R., I.E.S., D.A.S., M.S., J.C.S., F.S., T.S., D.V.S., J.S., P.M.T., M.T., J. Tolvanen, J. Török, M.v.d.P., L.V., M.E.V., D.F.W., N.T.W., J.W., K.W., A.G.W., A.W., D.W., M. Z. performed research and contributed the data; Z.J. calculated Human Footprint Indices; K.H. analysed the data; L.H. and K.H. wrote the manuscript, and all authors edited the manuscript. Valuable scientific contributions throughout the writing and editing process were done by D.A., J. Tolvanen, A. Millon, W.D.K., P.B., M.G., M.S., H. Pöysä, M.Ö., M.T., M.v.d.P., D.A.S., and A. Margalida.

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The authors declare no competing interest.

This article is a PNAS Direct Submission.

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