

PREDATION

Global pattern of nest predation is disrupted by climate change in shorebirds

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Ongoing climate change is thought to disrupt trophic relationships, with consequences for complex interspecific interactions, yet the effects of climate change on species interactions are poorly understood, and such effects have not been documented at a global scale. Using a single database of 38,191 nests from 237 populations, we found that shorebirds have experienced a worldwide increase in nest predation over the past 70 years. Historically, there existed a latitudinal gradient in nest predation, with the highest rates in the tropics; however, this pattern has been recently reversed in the Northern Hemisphere, most notably in the Arctic. This increased nest predation is consistent with climate-induced shifts in predator-prey relationships.

Climate change is affecting organisms at a global scale in several ways (1–4), including directly altering demographic parameters such as adult survival (5) and reproduction (1) or through altered trophic interactions (1, 6, 7). Successful recruitment counters mortality and maintains viable populations; thus, disruption of reproductive performance can have detrimental effects on wild populations (8–10). Alterations in demographic parameters have been attributed to recent climate change (1, 5, 11), especially in the Arctic, where the consequences of warming are expected to be more pronounced (6, 12). However, the evidence for impacts of climate change on species interactions is mixed, and to date there is no evidence that such interactions are changing globally (1–3).

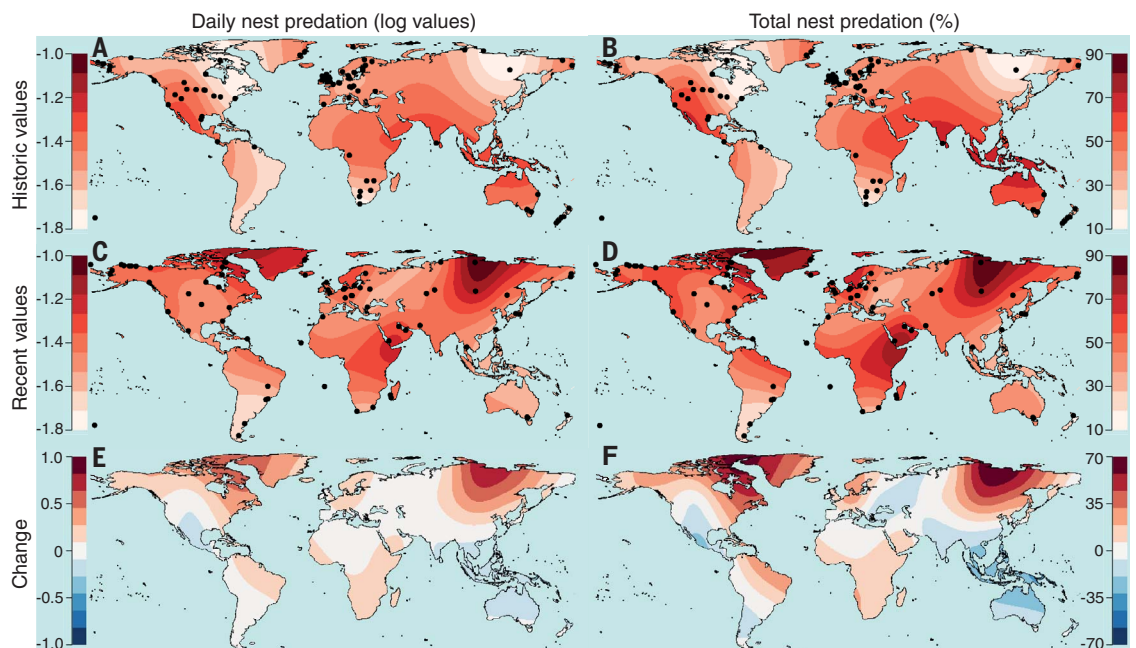
Offspring mortality due to predation has a pivotal influence on the reproductive performance of wild populations (8, 13–15), and extreme rates of predation can quickly lead to population declines or even species extinction (16). Thus, nest predation is a good indicator of the potential for reproductive recruitment in bird populations (10). Disruption to annual productivity through increased nest predation could have a detrimental effect on population dynamics and lead to increased extinction risks (9). To explore changes in spatial patterns of reproduction and potential alterations in trophic interactions due to changes in climate, we used nest predation data from shorebirds, a globally distributed group of ground-nesting birds that exhibit high inter-specific similarity in nest appearance to potential

predators and are exceptionally well-studied in the wild, including ecology, behavior, and demography (10, 17, 18). We collected data from both published and previously unpublished sources that included 38,191 nests in 237 populations of 111 shorebirds species from 149 locations, encompassing all continents across a 70-year time span (fig. S1 and table S1).

Using our comprehensive dataset in a spatio-phylogenetic framework (19), we show that rates of nest predation increased over the past 70 years. Daily nest predation, as well as total nest predation (reflecting the full incubation period for a given species), have increased overall worldwide since the 1950s (Figs. 1 and 2, A and B; fig. S2, A and B; and table S2). Thus, total nest predation was historically (until 1999) on average $43 \pm 2\%$ (SEM), and this has increased to $57 \pm 2\%$ since 2000. However, the extent of change shows considerable geographical variation. In the tropics and south temperate areas, changes in daily and

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Fig. 1. Nest predation in shorebirds. (A and B) Historic rates of nest predation (1944–1999, 145 populations). (C and D) Recent rates of nest predation (2000–2016, 102 populations). (E and F) Changes between historic and recent nest predation rates. Dots show study locations. [(A), (C), and (E)] Daily nest predation (log transformed) (materials and methods). [(B), (D), and (F)] Total nest predation (percentage) (materials and methods and fig. S1, geographic coverage).



total nest predation were not statistically significant, whereas in the north temperate zone, and especially the Arctic, the increase was pronounced (Figs. 1 and 2, A and B; fig. S2, A and B; and table S2). This pattern holds across major clades of shorebirds (Fig. 2, C and D; fig. S2, C and D; and table S3) and is also observed within local populations, with daily and total nest predation increasing significantly in well-monitored north temperate and Arctic breeding populations (Fig. 2, E and F). Thus, the total nest predation was historically $35 \pm 6\%$, which increased to $64 \pm 5\%$ in recent years for these long-term monitored populations (Fig. 2F and tables S4 and S5).

Life-history theory predicts that species that breed close to the equator should exhibit higher rates of nest predation than those of species that breed in temperate and polar latitudes, in part owing to the higher diversity of potential nest predators in the tropics, and there is an empirical support for this prediction (14, 15, 20, 21). In line with theoretical expectations, historic rates of nest predation in shorebirds follow the parabolic relationship between both daily and total rates of nest predation and latitude (Fig. 3, fig. S3, and table S6).

However, in recent years, daily nest predation changed only modestly in the tropics and Southern Hemisphere (Fig. 3 and fig. S3), although it increased nearly twofold in the North temperate zone and threefold in the Arctic compared with historic values (Figs. 2A and 3). Thus, 70% of nests are now being depredated in the Arctic (Fig. 2B). As a consequence of latitude-dependent changes in nest predation, predation rates now increase from the equator to the Arctic, in contrast to the historic parabolic latitudinal pattern (Fig. 3, fig. S3, and table S6). Although data from Southern Hemisphere are scanty, they suggest no major changes in nest predation in southern regions (Fig. 1).

It is thought that climate change has influenced trophic interactions (1, 6, 7, 12); therefore, to investigate whether altered rates of nest predation are driven by climate, we calculated the changes in ambient temperature in each shorebird population and tested whether the temperature changes predict the shifts in nest predation at a global scale (19). We used two proxies of climate change: the slope of annual mean temperature regressed against time and the standard deviation of annual mean temperatures measured over 30 years for each shorebird population. Higher rates of both daily and total nest predation were associated with increased ambient temperatures and temperature variations (Fig. 4). These results are robust to the choice of climatic variables over periods of 20, 30, or 40 years (table S7).

Because predation is the most common cause of breeding failure (13, 14), our results imply declining reproductive success in a widely distributed avian taxon. This decline, unless compensated by higher juvenile or adult survival and/or increased production of clutches, will drive global population declines when recruitment is not sufficient to maintain existing population

sizes (9, 10). However, adult survival of long-distance migrants is also decreasing because of recent habitat loss at staging areas (22, 23), and declining chick survival has been reported across

Europe (24). Therefore, high-latitude breeders are squeezed by both poor breeding performance and reduced adult survival. Although tropical shorebirds may increase the number of breeding

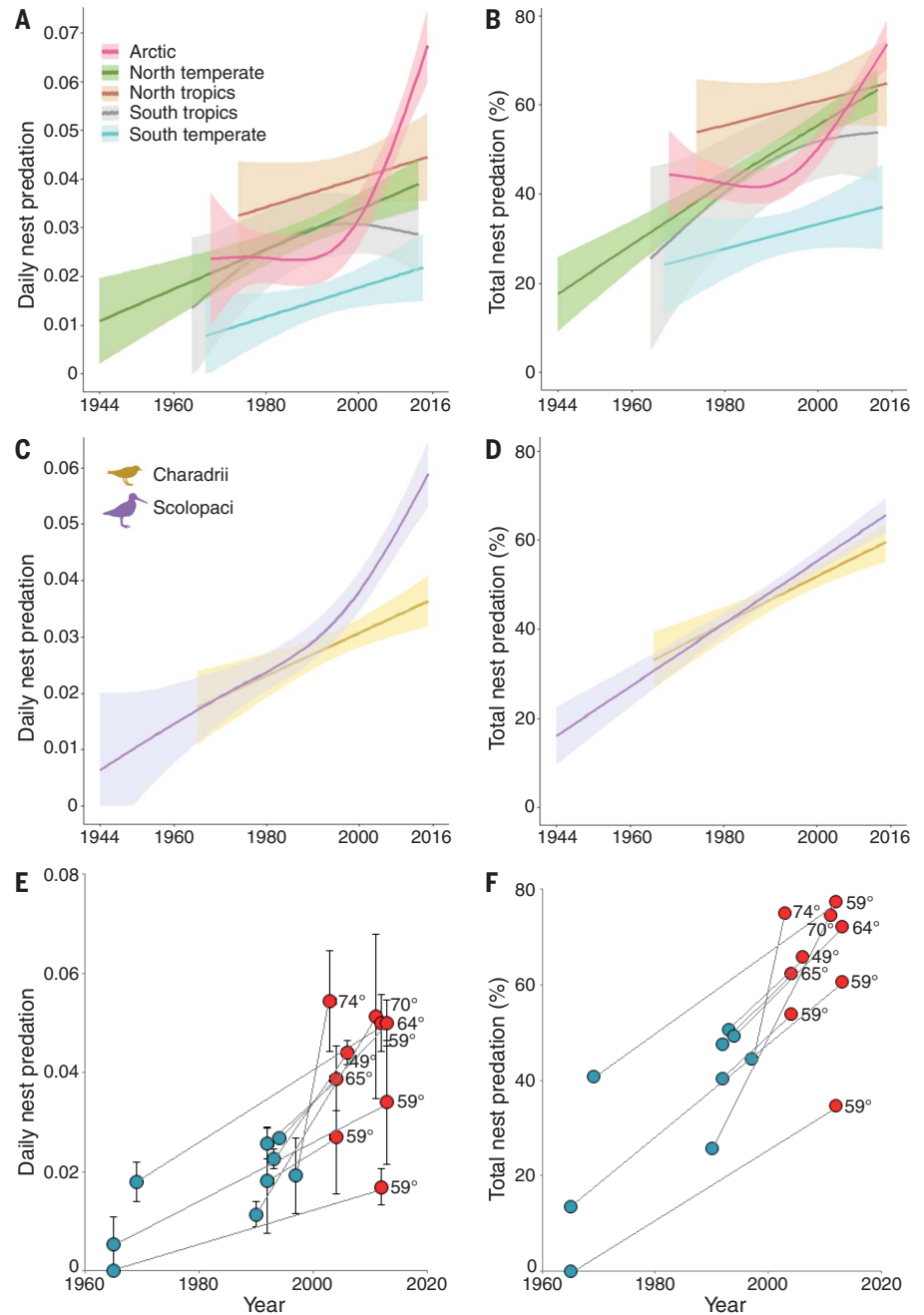


Fig. 2. Temporal changes in nest predation of shorebirds. (A and B) Nest predation rates for five latitudinal areas. Arctic, $n = 86$ populations; north temperate, $n = 96$ populations; north tropics, $n = 17$ populations; south tropics, $n = 14$ populations; south temperate, $n = 24$ populations. Area definitions are provided in (19), and model description is available in table S2. (C and D) Nest predation rates for plovers and allies (Charadrii, 110 populations) and sandpipers and allies (Scolopaci, 127 populations). Clade definitions are provided in (19), and model descriptions are available in table S3. (E and F) Local changes in nest predation rates for nine populations. Each dot represents mean \pm SEM (E) over 2 to 19 breeding seasons for historic data (blue) and recent data (red). Latitude of the population is given next to the recent data (tables S4 and S5, model descriptions). [(A) to (D)] Generalized additive model fits with 95% confidence intervals. [(A), (C), and (E)] Daily nest predation. [(B), (D), and (F)] Total nest predation.

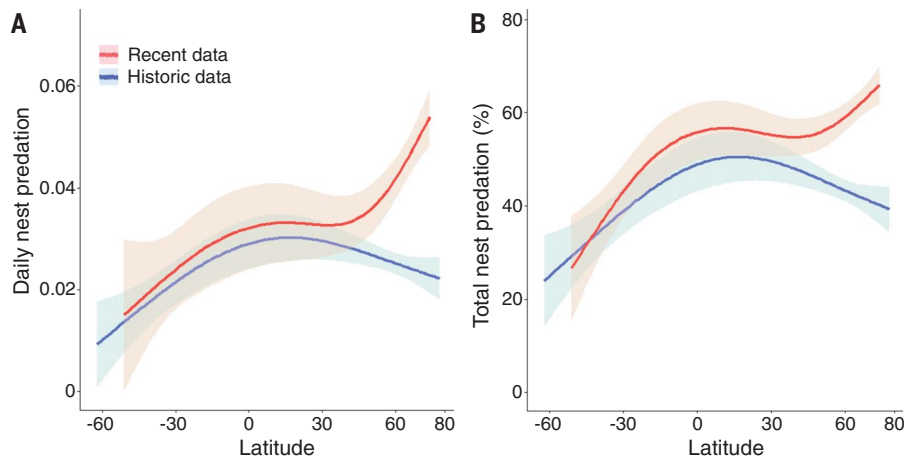


Fig. 3. Latitudinal gradient in historic versus recent nest predation of shorebirds. (A) Daily and (B) total nest predation rates (historic data 1944–1999, $n = 145$ populations; recent data 2000–2016, $n = 102$ populations), generalized additive model fits with 95% confidence intervals (table S6, model descriptions) (19).

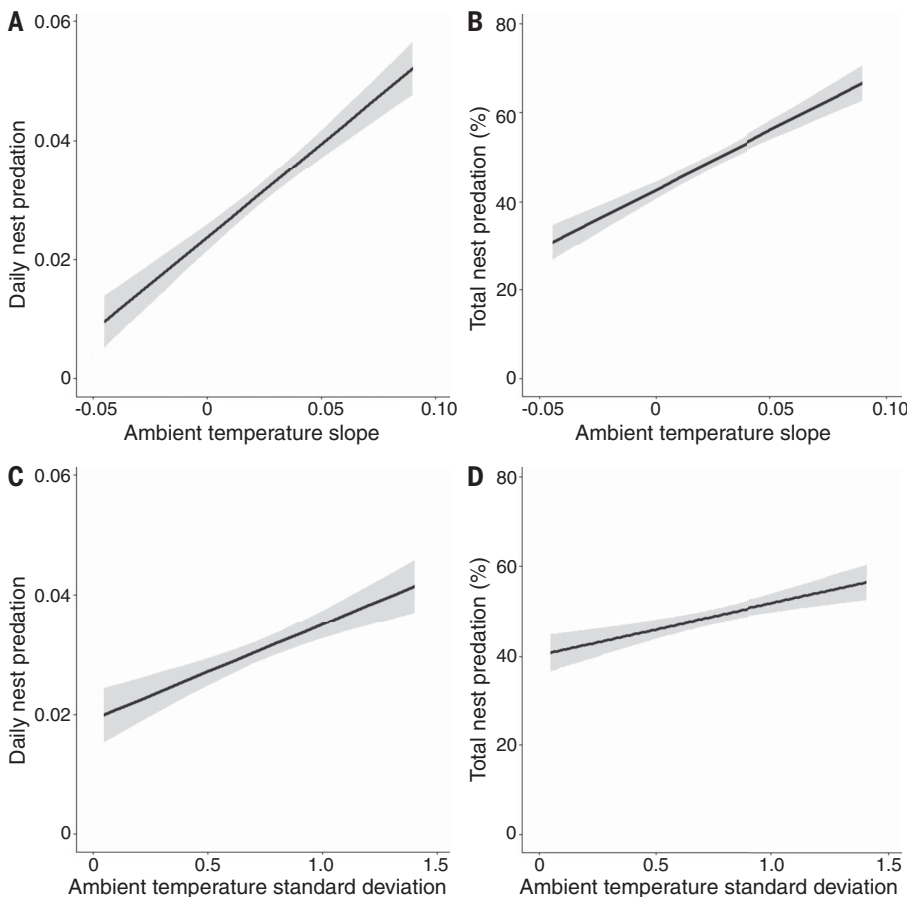


Fig. 4. Climate change predicts nest predation rates in shorebirds. (A and B) Relationship between (A) daily or (B) total nest predation rates and the slope of mean year temperatures. (C and D) Relationship between (C) daily or (D) total nest predation rates and the standard deviation of mean year temperatures. [(A) to (D)] Climatic data over 30 years before the last year of data collection; $n = 247$ values, generalized additive model fits with 95% confidence intervals (table S7, model descriptions) (19).

attempts and thus compensate for low breeding success, such compensation is limited at higher latitudes by short polar summers (6, 12). Because most shorebirds are already declining (18, 23, 25), our results suggest that an important correlate of this decline is the elevated nest predation.

Climate change may influence nest predation rates in several ways (1, 6, 12). First, lemmings (*Lemmus* spp. and *Dicrostonyx* spp.), small rodents that represent the key component of the Arctic food web, have experienced a crash in their abundances and population cycling due to unsuitable snow cover as a result of ambient temperature increase and fluctuations (26–28). This change was documented over vast Arctic areas around the year 2000 (26–28), and the pattern was similar for temperate voles in Europe (*Microtus* spp. and *Myodes* spp.) (29, 30). Changes in rodent abundances may have led to alterations in predator-prey interactions in the Northern Hemisphere, where predators who normally consume mainly rodents increased predation pressure on alternative prey, including shorebird nests (12, 28). Second, the behavior and/or distribution of nest predators may have changed because of climate change; for instance, the distribution or densities of nest predators such as foxes (*Vulpes* spp.) may have increased, or their behavioral activity have changed, making them more successful egg-consumers (4, 6, 12). Third, vegetation structure may have changed around shorebird nests, leading to increased predation (6, 12, 25).

The demographic changes we report here have two major implications. First, migrating birds have been presumed to benefit from breeding in the Arctic as a consequence of lower predation pressure (31). Currently, however, the productivity of Arctic populations is declining because of high rates of nest predation, which suggests that energy-demanding long-distance migration to northern breeding grounds is no longer advantageous from a nest predation perspective. Thus, the Arctic now represents an extensive ecological trap (32) for migrating birds, with a predicted negative impact on their global population dynamics. Second, Arctic birds are likely to decline in the future because of the synergistic effects of the climatically driven increase of predation pressure at their breeding grounds, a trophic mismatch during the chick-rearing period owing to delayed chick hatching relative to the peak of food abundance (6, 33), predicted shrinkage of suitable habitat (6, 12), and reduced adult survival during migration (22, 23). A future scientific challenge with crucial consequences for species conservation lies in disentangling the effects of these drivers on the overall viability of bird species.

We have demonstrated that rapid alterations in species interactions are occurring at a global scale and that these changes are related to altered climate. This underlines the need for understanding the effects of climate change not only for individuals and their populations but also for interactions in complex ecosystems, including prey and predators.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/362/6415/680/suppl/DC1
Materials and Methods
Figs. S1 to S3
Tables S1 to S8
References (35–218)

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No longer a safe haven

Many biological patterns have a latitudinal component. One long-recognized pattern is that predation rates are higher at lower latitudes. This may explain why many migratory birds travel thousands of miles from the tropics to the poles to breed. Looking across thousands of records, Kubelka *et al.* found that climate change seems to have altered this fundamental pattern. In shorebirds, at least, predation rates on nests are now higher in the Arctic than in the tropics.

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