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1 **Title: Global pattern of nest predation is disrupted by climate change in shorebirds**

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23 **Abstract:** Ongoing climate change is thought to disrupt trophic relationships with consequences for
24 complex interspecific interactions, yet the effects of climate change on species interactions are poorly
25 understood and such effects have not been documented at a global scale. Using a unique database of
26 38,191 nests from 237 populations, we found that shorebirds have experienced a worldwide increase in
27 nest predation over the last 70 years. Historically, there existed a latitudinal gradient in nest predation
28 with the highest rates in the tropics, however, this pattern has been recently reversed in the Northern
29 hemisphere, most notably in the Arctic. This increased nest predation is consistent with climate-induced
30 shifts in predator-prey relationships.

31 **One Sentence Summary:** Climate change increases offspring mortality in shorebirds globally.

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

40 Offspring mortality due to predation has a pivotal influence on the reproductive performance of
41 wild populations (8, 13–15) and extreme rates of predation can quickly lead to population declines or
42 even species extinction (16). Thus nest predation is a good indicator of the potential for reproductive
43 recruitment in bird populations (10). Disruption to annual productivity through increased nest predation
44 could have a detrimental effect on population dynamics and lead to increased extinction risks (9). To

45 explore changes in spatial patterns of reproduction and potential alterations in trophic interactions due to
46 changes in climate, we use nest predation data from shorebirds, a globally distributed group of ground-
47 nesting birds that exhibit high inter-specific similarity in nest appearance to potential predators and are
48 exceptionally well-studied in the wild including ecology, behaviour and demography (10, 17, 18). We
49 collected data from both published and previously unpublished sources that included 38,191 nests in 237
50 populations of 111 shorebirds species from 149 locations encompassing all continents across a 70-year
51 time span (fig. S1 and table S1).

52 Using our comprehensive dataset in a spatio-phylogenetic framework (19), we show that rates of
53 nest predation increased over the last 70 years. Daily nest predation, as well as total nest predation
54 (reflecting the full incubation period for a given species), have increased overall worldwide since the
55 1950s (Fig. 1, Fig. 2A, Fig. 2B, fig. S2A, fig. S2B and table S2). Thus total nest predation was
56 historically (until 1999) on average $43\% \pm 2\%$ (SEM), and this has increased to $57\% \pm 2\%$ since 2000.
57 However, the extent of change shows considerable geographical variation. In the tropics and South
58 temperate areas, changes in daily and total nest predation were not statistically significant, whereas in the
59 North temperate zone, and especially the Arctic, the increase was pronounced (Fig. 1, Fig. 2A, Fig. 2B,
60 fig. S2A, fig. S2B and table S2). This pattern holds across major clades of shorebirds (Fig. 2C, Fig. 2D,
61 fig. S2C, fig. S2D and table S3) and is also observed within local populations with daily and total nest
62 predation increasing significantly in well-monitored North temperate and Arctic breeding populations
63 (Fig. 2E and Fig. 2F). Thus the total nest predation was historically $35\% \pm 6\%$ that increased to $64\% \pm$
64 5% in recent years for these long-term monitored populations (Fig. 2F, table S4 and table S5).

65 Life-history theory predicts that species that breed close to the Equator should exhibit higher rates
66 of nest predation than species breeding in temperate and polar latitudes, in part owing to the higher
67 diversity of potential nest predators in the tropics, and there is an empirical support for this prediction (14,
68 15, 20, 21). In line with theoretical expectations, historic rates of nest predation in shorebirds follow the

69 parabolic relationship between both daily and total rates of nest predation and latitude (Fig. 3, fig. S3 and
70 table S6).

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

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

86 Since predation is the most common cause of breeding failure (*13, 14*), our results imply declining
87 reproductive success in a widely distributed avian taxon. This decline, unless compensated by higher
88 juvenile or adult survival and/or increased production of clutches, will drive global population declines
89 when recruitment is not sufficient to maintain existing population sizes (*9, 10*). However, adult survival
90 of long-distance migrants are also decreasing due to recent habitat loss at staging areas (*22, 23*), and
91 declining chick survival has been reported across Europe (*24*). Therefore, high latitude breeders are
92 squeezed by both poor breeding performance and reduced adult survival. Whilst tropical shorebirds may

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

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

109 The demographic changes we report here have two major implications. First, migrating birds have
110 been presumed to benefit from breeding in the Arctic as a consequence of lower predation pressure (31).
111 Currently, however, the productivity of Arctic populations is declining due to high rates of nest predation,
112 which suggests that energy demanding long-distance migration to northern breeding grounds is no longer
113 advantageous from a nest predation perspective. Thus the Arctic now represents an extensive ecological
114 trap (32) for migrating birds with a predicted negative impact on their global population dynamics.
115 Second, Arctic birds are likely to decline in the future due to the synergistic effects of the climatically-
116 driven increase of predation pressure at their breeding grounds, a trophic mismatch during chick rearing

117 period due to delayed chick hatching relative to the peak of food abundance (6, 33), predicted shrinkage
118 of suitable habitat (6, 12) and reduced adult survival during migration (22, 23). A future scientific
119 challenge with crucial consequences for species conservation lies in disentangling the effects of these
120 drivers on the overall viability of bird species.

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

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608 Climatic data are freely available at <http://www.cru.uea.ac.uk/data>. Sources of primary nest predation
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610 [provide the Dyad number soon.](#)

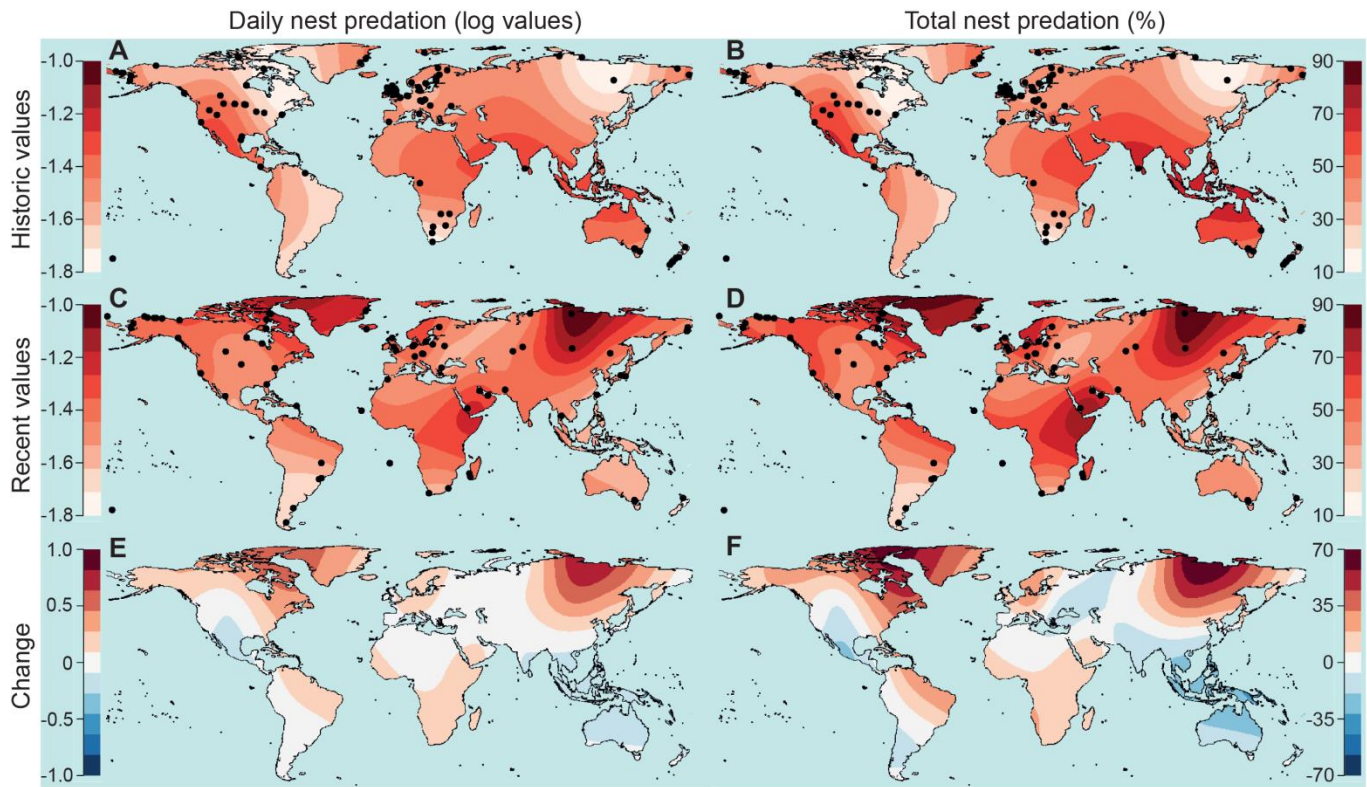
611 **Supplementary materials:**

612 Materials and Methods

613 Figures S1 to S3

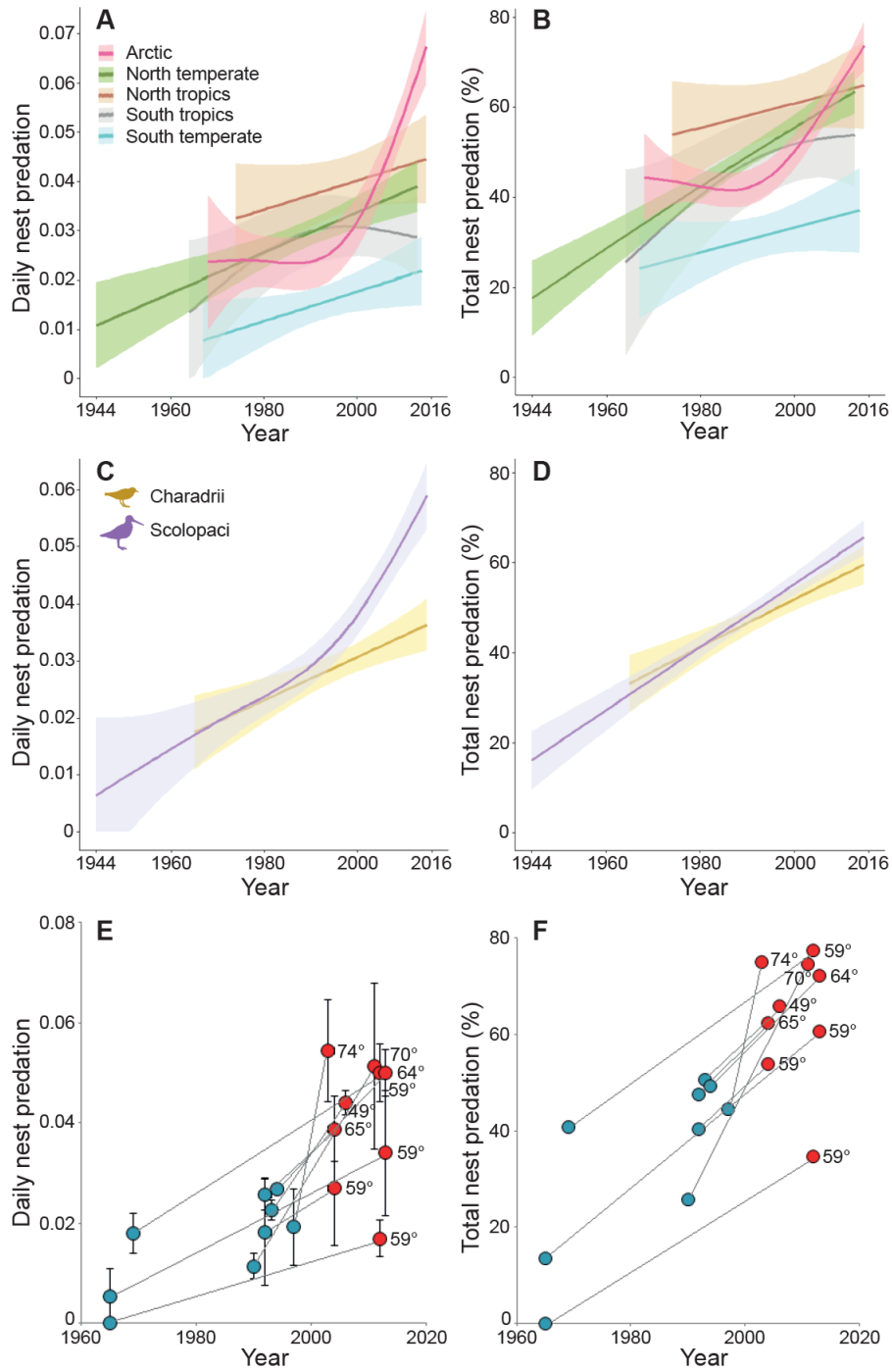
614 Tables S1 to S8

615 References (34–217)



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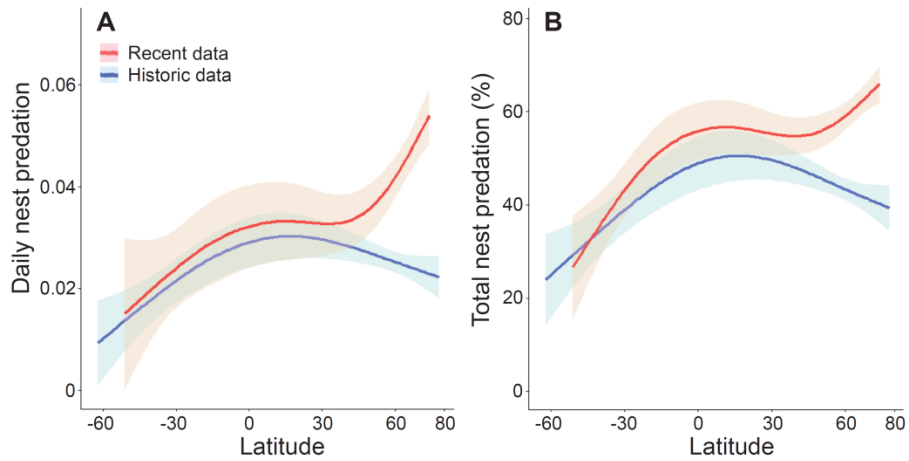
617 **Fig. 1. Nest predation in shorebirds.** (A and B) Historic rates of nest predation (1944–1999, 145
 618 populations). (C and D) Recent rates of nest predation (2000–2016, 102 populations). (E and F) Changes
 619 between historic and recent nest predation rates. Dots show study locations. (A, C,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



622

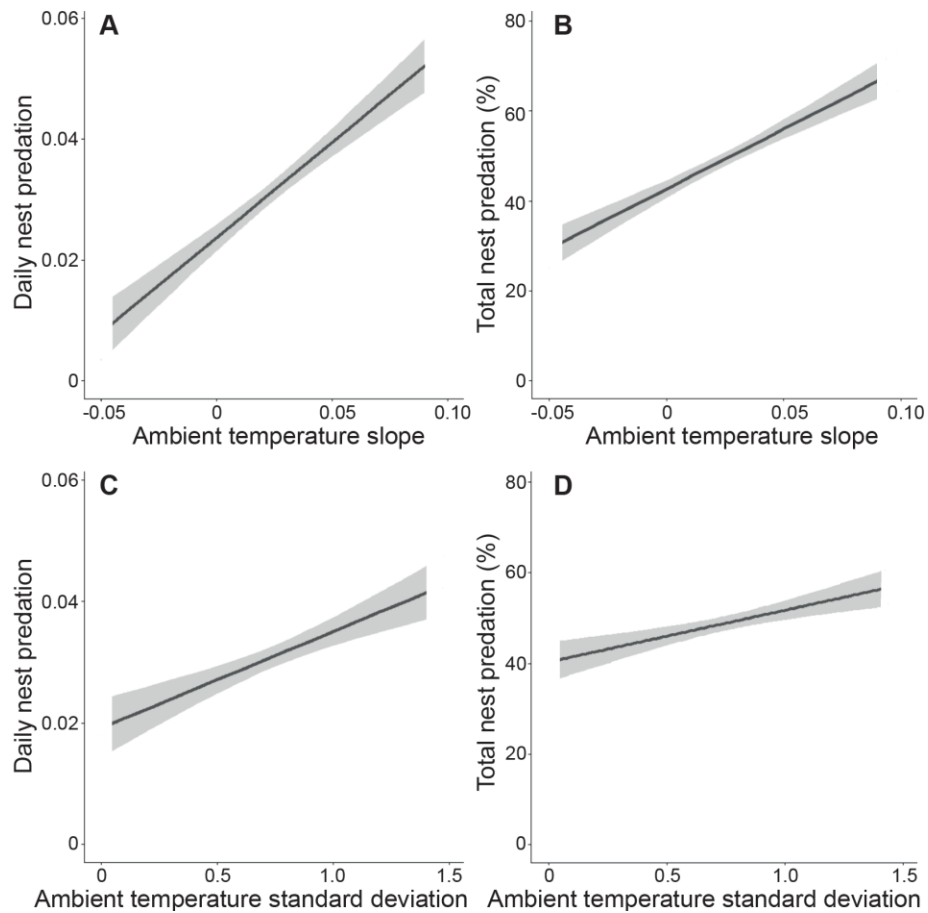
623 **Fig. 2. Temporal changes in nest predation of shorebirds.** (A and B) Nest predation rates for five
 624 latitudinal areas (Arctic n = 86 populations, North temperate n = 96 populations, North tropics n = 17
 625 populations, South tropics n = 14 populations, South temperate n = 24 populations), see (19) for areas
 626 definition and model description in table S2. (C and D) Nest predation rates for plovers and allies

627 (Charadrii = 110 populations) and sandpipers and allies (Scolopaci = 127 populations), see (19) for clades
628 definition and models description in table S3. (E and F) Local changes in nest predation rates for nine
629 populations, each dot represents mean \pm SEM (E) over 2–19 breeding seasons for historic data (blue) and
630 recent data (red), latitude of the population is given next to the recent data, see table S4 and models
631 description in table S5. (A–D) Generalized additive model fits with 95% confidence intervals. (A, C and
632 E) Daily nest predation. (B, D and F) Total nest predation.



633

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



638

639 **Fig. 4. Climate change predicts nest predation rates in shorebirds.** (A and B) Relationship between
 640 daily (A) or total (B) nest predation rates and the slope of mean year temperatures. (C and D)
 641 Relationship between daily (C) or total (D) nest predation rates and the standard deviation of mean year
 642 temperatures. (A–D) Climatic data over 30 years prior to the last year of data collection, $n = 247$ values,
 643 generalized additive model fits with 95% confidence intervals, see (19) for details and table S7 for model
 644 descriptions.