11-15-2017

Annual global mean temperature explains reproductive success in a marine vertebrate from 1955 to 2010

Robert A. Mauck
Kenyon College

Donald C. Dearborn
Bates College, ddearbor@bates.edu

Charles E. Huntington
Bowdoin College

Recommended Citation

Mauck RA, Dearborn DC, and Huntington CE. 2018. Annual Global Mean Temperature explains reproductive success in a marine vertebrate from 1955-2010. Global Change Biology 24:1599-1613.

Title:

Annual Global Mean Temperature explains reproductive success in a marine vertebrate from 1955-2010

Authors:
Robert A. Mauck[1], Donald C. Dearborn[2], Charles E. Huntington[3]
[1]Biology Department, Kenyon College, Gambier, OH 42022
[2]Biology Department, Bates College, Lewiston, ME 04240
[3]Biology Department, Bowdoin College, Brunswick, ME 04011

Corresponding author email: mauckr@kenyon.edu
Corresponding author telephone: 740-427-5076

Running head: Global temperature and reproductive success

Keywords: climate change, Global Mean Temperature, air temperature, sea-surface temperature, seabirds, storm-petrels, long-term dataset, longitudinal study, age-effects

Paper Type: Primary Research

Word Count (Intro, Methods, Results, Discussion, Acknowledgements): ~ 5920

ABSTRACT

The salient feature of anthropogenic climate change over the last century has been the rise in global mean temperature. However, global mean temperature is not used as an explanatory variable in studies of population-level response to climate change, perhaps because the signal to noise ratio of this gross measure makes its effect difficult to detect in any but the longest of datasets. Using a population of Leach's storm-petrels breeding in the Bay of Fundy, we tested whether local, regional, or global temperature measures are the best index of reproductive success in the face of climate change in species that travel widely between and within seasons. With a 56-year dataset, we found that Annual Global Mean Temperature (AGMT) was the single most important predictor of hatching success, more so than regional sea surface temperatures (breeding season or winter) and local air temperatures at the nesting colony. Storm-petrel reproductive success showed a quadratic response to rising temperatures, in that hatching success increased up to some critical temperature, then declined when AGMT exceeded that temperature. The year at which AGMT began to consistently exceed that critical temperature was 1988. Importantly, in this population of known-age individuals, the impact of changing climate was greatest on inexperienced breeders: reproductive success of inexperienced birds increased more rapidly as temperatures rose and declined more rapidly after the tipping point than did reproductive success of experienced individuals. The generality of our finding that AGMT is the best predictor of reproductive success in this system may hinge on two things. First, an integrative global measure may be best for species in which individuals move across an enormous spatial range, especially within seasons. Second, the length of our dataset and our capacity to account for individual- and age-based variation in reproductive success increase our ability to detect a noisy signal.

INTRODUCTION

The salient feature of anthropogenic climate change over the last century has been the rise in global mean temperature. This change has accelerated since the 1950s (IPCC, 2013). When viewed as a whole, the effects of rising global temperatures on the natural world have been profound (Rosenzweig *et al.*, 2008). However, direct evidence for these effects on biological systems is generally based on regional or local measures of temperature (Root *et al.*, 2003). Global mean temperature itself generally does not appear as an independent variable in these studies perhaps because the signal to noise ratio of this gross measure makes its effect difficult to detect in any but the longest of datasets. Global temperature is an index of an entire planet's worth of interactions. It is the great integrator. As such, it may explain more variation in the response of natural populations to climate change than do more proximate measures, particularly for animals that move over large spatial scales.

Annual Global Mean Temperature (AGMT) is a single, broad-brush metric that has risen by more than 0.6° C since 1950 (IPCC, 2013). AGMT is derived from a combination of marine and terrestrial temperatures (Hansen *et al.*, 2006). Both air and sea temperatures around the world have risen in parallel with global temperature, though the correlations between air, sea, and global temperatures are not perfect and vary around the globe (IPCC, 2013). Local climate at any particular place and time may not be in sync with the global mean. For organisms with restricted movement patterns such as flowering plants (Fitter & Fitter, 2002), insects (Pollard & Moss, 1995), or resident birds (Santisteban *et al.*, 2012), local or regional temperatures may be better predictors of reproductive success than global temperature. Even for migrant species that travel great distances between breeding and wintering sites, local temperatures at either site might best explain reproductive success if the movement within the breeding site is restricted

(Dyrcz & Halupka, 2008). For cosmopolitan species that travel widely between and within seasons, one can imagine a complex model that integrates precise measures of an individual's location and local temperature for every hour of every day over the course of a year. Even if possible, it is not clear that such a model would capture the conflicting effects of temperature within systems or the myriad combinations of direct and indirect effects across time. AGMT is a single metric that integrates across time and space and, therefore, may be well-suited for examining the effects of climate on species that cover great distances, both between and within seasons.

Marine vertebrates, in general, fit this criterion (Sydeman *et al.*, 2015). In addition, a number of marine vertebrate species breed on land and forage at sea and are susceptible to change in both regional sea surface temperatures and local air temperatures. Examples include pinnipeds (McDonald *et al.*, 2012) and sea turtles (Perez *et al.*, 2016, Saba *et al.*, 2012, Tomillo *et al.*, 2014), but seabirds are the most numerous and wide-spread vertebrate taxa to straddle both marine and terrestrial ecosystems worldwide (Schreiber & Burger, 2002). In fact, seabirds are renowned for the distances travelled within and between seasons (Weimerskirch *et al.*, 2012). Seabirds forage daily hundreds or thousands of kilometers from their nesting islands and also make large-scale migrational movements during the non-breeding portion of their annual cycle (Dearborn *et al.*, 2003, Egevang *et al.*, 2010, Pollet *et al.*, 2014). Long-term studies of seabirds, therefore, should provide appropriate conditions with which to detect the effect of global temperatures on reproductive success in natural populations.

Seabirds are known to be sensitive to ecosystem change, both natural and anthropogenic (Frederiksen *et al.*, 2004, Sandvik *et al.*, 2012, Sydeman *et al.*, 2012, Sydeman *et al.*, 2015, Sydeman *et al.*, 2017). Ninety percent of the studies on seabirds that examined sea surface temperatures (SST) showed a negative correlation with survival and 70% showed a negative effect on reproduction. Such effects are best documented in the mid- and high latitudes (Root *et al.*, 2003, Sydeman *et al.*, 2012, Valtonen *et al.*, 2014) and a meta-analysis of 29 North Atlantic seabird species suggests that the strongest effect of climate variability is on reproduction rather than survival (Sandvik *et al.*, 2012).

Generally, the effects of rising SST are indirect, manifested through availability and quality of prey species (Kawaguchi *et al.*, 2013). Warming SSTs are often associated with lowered availability of zooplankton at critical times (Friedland *et al.*, 2012, Hunt *et al.*, 2011, Mackas *et al.*, 2007). Responses by seabirds to such warming include changes in incubation behavior (Shoji *et al.*, 2012), changes in breeding phenology (Burthe *et al.*, 2012, Chambers *et al.*, 2013), lowered probability of breeding (Cubaynes *et al.*, 2011), early-life survival and recruitment (Fay *et al.*, 2017, Pardo *et al.*, 2017), and reduced reproductive success in general (Rolland *et al.*, 2010). In the western Atlantic, for example, distributions of many demersal fishes (Nye *et al.*, 2009) and entire fish communities (Lucey & Nye, 2010) have shifted northward and into deeper waters over the past five decades in response to warming ocean temperatures.

While the effect of rising SST on seabird reproduction has been well studied, less attention has been paid to the effect of air temperature (AT) on seabird reproduction (Fagundes *et al.*, 2016, Sydeman *et al.*, 2012), though terrestrial systems' response to such warming is well documented (e.g., Lebreton, 2011, Santisteban *et al.*, 2012). Rising air temperatures impose direct thermal effects on marine vertebrates that breed on land and forage at sea (Croxall *et al.*, 2002). These local effects can be negative or positive and may differ from indirect effects manifested in the community on which they forage. Although, warming air temperatures have been shown to impose heat stress on nestling birds (Boersma & Rebstock, 2014, Hart *et al.*, 2016), particularly in tropical regions, warming air temperatures in the mid- and high latitudes may reduce the cost of thermoregulation on land during the breeding season and be a net benefit (Olsen & Baker, 2001).

Given the natural inter-annual variation in climate and biological systems, only very long-term studies have the power to reveal the effect of global mean temperature on natural populations. Long-term studies that track presence/absence or population size can reveal how species distributions or abundances change over time (Bussiere *et al.*, 2015, Cunningham & Moors, 1994). However, only studies that track individuals through time allow us to account for intrinsic factors such as age and individual quality before analyzing changes due to climatic factors. Although such long-term biological studies on terrestrial systems are vastly more common than on marine systems (Rosenzweig *et al.*, 2008), few exceed a half-century in length. Such multi-decadal, individual-based studies provide the best opportunity to assess the utility of global temperature in explaining a species' response to climate change.

The breeding population of Leach's storm-petrels (*Oceanodroma leucorhoa*) at the Bowdoin Scientific Station at Kent Island in the Bay of Fundy has been monitored with marked individuals since 1955. Storm-petrels breed in the North Atlantic after spending the winter in the equatorial Atlantic (Pollet *et al.*, 2014). These seabirds produce a single egg per year for up to 38 years (Huntington *et al.*, 1996), and incubating adults travel up to 2600 km during a single foraging trip (Mauck *et al.*, 2016). Hatching success has been shown to vary with individual quality (Mauck *et al.*, 2004) and to increase with experience (Mauck *et al.*, 2012). This latter point is important, as inexperienced individuals of a species may also be less buffered against environmental stressors (Bunce *et al.*, 2005), in which case we predict that any negative effects of climate change might disproportionately affect inexperienced breeders in our population. Overall, the confluence of a highly mobile vertebrate and a population that has been studied for over half a century provides a rare opportunity to test the hypothesis that global mean temperature may be the best integrator of global climate change and should, therefore, best predict the relationship between changing climate and reproductive success in natural populations.

Given that these pelagic seabirds travel long distances both within and between seasons, as well as forage at sea and breed on land, we expect that the integrated index of AGMT will explain more variation in reproductive success than will either local air temperatures or regional sea surface temperatures. We also expect that rising local air temperatures will provide a direct positive thermal benefit to incubating adults and, though not as strong a signal as global temperature, should positively affect reproductive success in this marine vertebrate. Since most studies show a negative effect of rising SST on seabird reproductive success, we expect the effect of SST on storm-petrel biology to be negative. If local and regional effects are opposite and of equal strength, it is possible that they will cancel each other out such that no effect of global temperature will be evident. It is also possible that the effect of either local or regional temperatures will be strong enough alone to explain reproductive success in these seabirds. Finally, the combination of air and sea surface temperatures together may obviate the need for AGMT to explain reproductive success in this marine vertebrate. To test these contrasting predictions, we modeled global, regional, and local temperature effects, both linear and quadratic, against storm-petrel reproductive output from 1955 through 2010.

METHODS

The study species and population

CEH began the study of the breeding population of Leach's storm-petrels at the Bowdoin Scientific Station at Kent Island, New Brunswick, Canada (44° 35' N, 66° 45' W) in 1955. Kent Island is an 85-ha island in the Grand Manan Archipelago at the mouth of the Bay of Fundy. Approximately 15,000 pairs nest on Kent Island (Minnich, unpubl.) of which 300-600 burrows have been monitored annually in four non-contiguous study sites on the island.

Leach's storm-petrels are long-lived pelagic seabirds of the order Procellariiformes, all of which share the life history traits of long life span, deferred reproduction and a single egg clutch. The 45-g storm-petrels nest in underground burrows, primarily on the northern half of Kent island in forest of spruce, fir, and mixed hardwood. Most eggs are produced from late May through early July.

Adults are monomorphic and males and females alternate incubation duties during a 40- to 44-day incubation period (Huntington *et al.*, 1996). The incubating adult fasts for up to seven days (3.3 ± 0.6 SD days), losing up to 7.5% of its body mass daily while its partner forages at sea (Mauck *et al.*, 2011, Ricklefs, 1986, Zangmeister *et al.*, 2009). Once hatched, the nestling is brooded for 3–8 days, after which it remains alone in the burrow for an additional 60–70 days and is fed during brief nocturnal visits by both parents (Mauck & Ricklefs, 2005). Producing a single chick requires over 100 days of parental effort and failed adults generally do not make a second attempt in one season.

Incubation is often considered the most energetically demanding phase of seabird reproduction (Barbraud, 2000, Weimerskirch, 1990, Weimerskirch *et al.*, 2012). This may explain why variation in the ability of adults to successfully hatch an egg (mean 76%) has a greater impact on annual reproductive success on Kent Island (Huntington *et al.*, 1996) than does raising a chick to independence (mean 93%). Hatching success is largely a function of the pair's ability to cope with the energetic demands of incubation (Zangmeister *et al.*, 2009), which may rest on each adult's ability to locate and store energy or on the degree to which the adult reduces its own energy reserves. Given its primacy in determining reproductive success and the continuity of the data collected, we used hatching success to gauge reproductive success in this population.

Determining hatching success and breeding experience

With the exception of 1977, incubating adults sitting on eggs were captured and identified in each burrow during June and July from 1955 to 2010. Unbanded individuals were fitted with unique USFWS (U.S. Fish and Wildlife Service) / CWS (Canadian Wildlife Service) bands. Hatching success (0 or 1) was determined in late August/early September by the presence or absence of a chick where previously there had been an egg. Because extra-pair paternity is rare or absent in this population (Dearborn *et al.*, 2015, Mauck *et al.*, 1995), we assumed all eggs were the product of the attending adults. In this fashion, we recorded hatching success and breeding experience for 25,879 adult-burrow-years from 1955 through 2010.

Measures of climatic conditions - global temperature

We used data from National Oceanic and Atmospheric Administration (NOAA) to characterize temperature on a global scale. The Global Surface Temperature combines Land and Sea Surface temperatures across a 5x5 degree world-wide grid to derive a single value that characterizes the temperature of the earth's surface in monthly intervals. The Global Temperature Anomaly is the temperature in any particular year minus a reference temperature. We used version 4.01 (https://www.ncdc.noaa.gov/data-access/marineocean-data/noaa-global-surface-temperature-noaa globaltemp), which used the years 1971–2000 to derive the mean reference temperature, which we refer to as Global Mean Temperature. For our analysis, we obtained 3 measures for each year from 1955 to 2010: Annual Global Mean Temperature (AGMT) and Breeding Season Mean Temperature (BSMT; May, June, July– incubation period), as well as the 5-year average of the AGMT based on the 5 years prior to each year of the study (5yrM).

Measures of climatic conditions - sea surface temperatures

We characterized Sea Surface Temperatures during the summer breeding season with mean monthly temperatures during May, June, and July; this span included the month before eggs were laid through the end of incubation. Breeding season SST (SST_b) were taken from the area bounded -69.5°E, 40.0°N, -65.5°E, 43.5°N (Mauck *et al.*, 2016). Because winter environmental conditions may affect adult physiological condition when they initially arrive on the breeding ground, we also included SST from the previous winter (December, January, February). For winter SST (SST_w), we used the mean of the previous December, January, and February temperatures bounded by -34.0°E, -15.0°N, -18.0°E, 20.0°N (Pollet *et al.*, 2014). We obtained raw SST data from the Hadley Centre Sea Ice and Sea Surface Temperature data set (Rayner *et al.*, 2003; www.metoffice.gov.uk/hadobs/hadisst).

Measures of climatic conditions - local temperatures

Daily weather data during the breeding season have been collected at Kent Island annually since 1939 (Cunningham, 1998). Temperature (Max, Min, Current) was recorded at

8AM and 8PM using analog thermometers. Daily Mean Temperature at Kent Island is calculated as the mean of the Minimum and Maximum temperatures for each 24-hour period. We used Mean Temperature to represent daily local air temperatures at Kent Island. To capture each season's local temperature at Kent Island, we calculated the mean of the mean monthly temperatures for June and July of each year.

In some years, Kent Island weather data are incomplete. For those missing values, we used weather data from Yarmouth, NS (Environment Canada; http://climate.weather.gc.ca/historical_data/search_historic_data_e.html) to estimate missing weather data on Kent Island. Yarmouth (43.83°N, -66.09°W; 96 km SSE of Kent Island) is the nearest coastal weather station for which continuous weather data are available from 1950 onward and for which mean temperature in the summer is highly correlated with Kent Island temperatures ($r = 0.78$, RAM). We modeled 56 years of summer Kent Island weather variables as a function of the corresponding weather variables at Yarmouth. We then used the resulting regression equations to convert Yarmouth temperatures to the corresponding missing Kent Island temperatures.

Statistical Analyses

Overview of modeling strategies - We followed a three-step strategy to evaluate the effect of temperature on reproductive success. We began by identifying an "Intrinsic" model that included only non-temperature related variables that might reasonably explain variation in reproductive success. The intrinsic model served as the base on which all further climate models were built and served as the NULL model against which we compared candidate models that included climate variables.

Because constructing all possible models from all possible forms (linear, quadratic, etc.) of every category of climate variable (Global, Regional/SST, Local/Kent Island) would produce an unmanageable number of models, we did an initial screening of each category of climate variable. For each, we constructed an array of expressions of that variable, from which we selected the most useful representative of that category for explaining storm-petrel reproductive success. The most useful form of each category was then included in further investigations.

We then constructed models representing all possible combinations of the variables that passed the initial screening plus the NULL/Intrinsic model. From these combinations, we compared the utility of each climate variable using an information theoretic approach. Because breeding experience increases storm-petrel hatching success (Mauck *et al.*, 2012) and other studies have shown that inexperienced individuals can be more susceptible to temperature variation than experienced individuals (Oro *et al.*, 2010), we further examined the best model from the final analysis for possible interactions with fixed effects in our intrinsic model.

Statistical procedures and model selection

We used the lme4 (Bates *et al.*, 2011) package in R (R Core Team, 2015) to construct generalized linear mixed-effects models (GLMM) for all candidate models. To assess hatching success (0 or 1), we used the glmer function with a logit link and binomial error term. We verified the assumptions of hatching success models by assessing over-dispersion using the R package RVAideMemoire (Hervé, 2017). To detect issues of collinearity, we calculated Variance Inflation Factors (vif function in lme4) for important models. We used the Effects Package, version 3.1-2 (Fox & Hong, 2009) to visualize isolated effects within the best models. We used normalized values for all climate variables to prevent convergence problems while running models.

We assessed model utility by evaluating Akaike's Information Criterion (AIC) and used sample size correction (AICc) for model selection (Burnham *et al.*, 2002). When calculating the AICc, the appropriate sample size for statistical evaluations of mixed effects models is not clear (Maas & Hox, 2005). While there were 25K instances of burrow-years, there were only 6K birds, 1400 burrows, and 56 years of data. Any of those might have served for the sample size. However, because burrow characteristics are known to affect reproductive success and are consistent between years (Fricke *et al.*, 2015), we used number of burrows as a conservative, and reasonable sample size for AICc calculation. During initial screening, we simply selected the model in each climate category with the lowest AICc for further consideration in the final analysis.

When choosing among competing models in the final analysis, we followed (Burnham *et al.*, 2002). When considering a set of models, we consider the model with the lowest AICc as the "best" model. Models with a difference in AICc (dAICc) < 2.0 are considered roughly equivalent. We refer to all models with dAICc < 4.0 of the best model as the set of "top" models, since 4.0 is often considered the cut-off point for reasonable models (Burnham *et al.*, 2002) .

Akaike model weights (ω) were calculated to rank models. We used the resulting parameter weights to further delineate between variables of interest and to derive weighted estimates of model parameters (Burnham *et al.*, 2002) from the set of candidate models. We calculated weighted parameter estimates using both the zero and the natural method (Grueber *et al.*, 2011) because we wanted to assess both the effects relative to the importance of all the models (zero method) and their effect as reflected only when included in models (natural method).

Modeling Hatching Success

Determining the intrinsic model

We constructed a full GLMM model that included adult Breeding Experience (BE; ordinal variable 1, 2, 3+, after Mauck *et al.*, 2012) and Pairbond Length (PBLen; ordinal 1, 2, 3+) as fixed effects. We included Adult_ID as a random effect to account for the effect of individual quality (Mauck *et al.*, 2004, Mauck *et al.*, 2012). We included Paribond_ID and Burrow_ID to account for non-independence and variation in the quality of each variable. We included Year as a categorical random effect to account for unmeasured characteristics of that year. We examined reduced models containing all combination of the fixed effects, each of which contained all the random effects. We chose the model with the lowest AICc as our Intrinsic model. All subsequent climate models included the random and fixed effects represented in the Intrinsic model.

Initial screening of climate variables

For Global Temperature, we compared the following variables: AGMT, Breeding Season (May, June, July) Global Mean (BGMT), and 5-Year Average Annual Mean (5yr AGMT). We examined SST during both breeding and winter seasons. For local temperature, we examined Kent Island Mean Temperatures during June and July. We examined both linear and quadratic forms for each temperature scale.

Final analysis of climate variables

From those variables identified in the initial screening, we constructed all possible models from that set of variables plus the NULL/Intrinsic model. All models in the analysis included the fixed and random effects identified in the Intrinsic model in addition to the added climate variables. By constructing all possible models from the representative local, regional, and global temperatures, we derived a set of seven models balanced in their representation of each climate variable. One model contained three temperature variables, three utilized subsets of two temperature variables, and three models contained only one temperature variable. Each temperature variable, therefore, appeared in four models.

RESULTS

General

Climate variables

Climate variables measured between 1955 and 2010 were normally distributed as evidenced by the low values for skew and kurtosis (Table 1). Temperature generally increased with time and there was some correlation between climate variables (Figure 1; Table 2). Highest among those was the correlation between local air temperatures on Kent Island (KI) and breeding season SST temperatures (SST_b). No correlation between temperature categories (local, regional, global) exceeded 0.8. To check for multi-collinearity issues, we calculated Variance Inflation Factors for important final models (see below).

Model assumptions

In every candidate model in every analysis, there was no evidence of over dispersion ($0 < Phi < 1$ in all cases). We calculated Variance Inflation Factors (VIF) for the top two models in the final analysis. All VIFs in the best model were under 1.63; in the full model, VIF of Local and SST were between 2.0-3.0, suggesting some collinearity between those two variables, but within an acceptable range (O'Brien, 2007).

Intrinsic Model for Hatching Success

The best model of hatching success without reference to temperature, contained Individual_ID, Burrow, Year and Pairbond_ID as random effects and Breeding Experience as the lone fixed effect (Table 3). Although the model with BE and PBLen was nearly as useful (dAICc = 1.03), the effect of PBLen in that model was relatively weak (-0.01 ± 0.01SE HS, Z = -0.80) compared to the effect of BE (0.15 ± 0.04SE HS, Z = 3.91). We, therefore, used the best model as our Intrinsic Model. (NOTE: sample size for this step was less than for all other steps because PBLen was known for only 24,198 burrow-years).

Initial Screening of Temperature Variables

Initial screening– global temperature

The quadratic form of the Annual Global Mean Temperature anomaly was clearly better than all other forms of Global Temperature. No other forms of the Global Temperature Anomaly had an AICc less than two from the quadratic form (Table 4). The relative importance of the AGMT was confirmed by model-averaged parameter weights such that AGMT (0.8) was more than four times that of BGMT (0.2) and the 5-Year Global Average (0.0) was not useful at all. Thus, the quadratic form of AGMT represented global temperatures in the final analysis.

Initial screening – sea surface temperatures

The best model contained only the linear form of breeding season SST (Table 5). Models containing only SST_b accounted for 0.941 of the cumulative model weights, compared to 0.06 for SST_w, further reinforcing the selection of breeding season SST as the appropriate indicator of Regional Temperatures for inclusion in the final analysis.

Initial screening – local (Kent Island) air temperature

The simple linear model of Mean Kent Island temperature was better than the quadratic form (dAICc = 1.83) (Table 6) and, therefore, was used in the final analysis.

Final Analyses

Final analyses – global, regional SST, local air

The quadratic form of AGMT (Figure 2) was in every top model (i.e., dAICc < 4.0 of the best model; Table 7), which drove its parameter weight (*w*) of 1.0 (Table 8). Local Kent Island temperatures (*w* = 0.69) had substantial value in explaining hatching success. Summer SST, was also useful, but less so (*w* = 0.37). In all, four models were within dAICc = 4.0 of the best model. The model with AGMT as the lone climatic variable had an effect sufficiently strong to appear in the top models (dAICc < 4.0). No other model with a single climate variable had a dAICc < 13. Clearly, Annual Global Mean Temperature is the single most important predictor of reproductive success in Leach's storm-petrels over the 56 year span covered by this study.

The full model (Global + Local + SST) was nearly as strong (dAICc = 0.72) as the best model that contained only AGMT and local Kent Island air temperatures. Effect estimates for AGMT and Kent Island temperatures were similar in both the full model (Table 9) and the best model (Table 10).

Examination of the full model fixed effects (Table 9) summarizes the relative contributions of each of the climate variables in the final analysis. As in every model with AGMT, both the linear (Z = 2.31) and quadratic (Z = -3.29) portions of the AGMT were strong, demonstrating increasing hatching success with temperature followed by a decline after some threshold was reached (Figure 2). The positive effect of Kent Island temperature was strong (0.29 ± 0.14SE HS, Z = 2.12; Figure 3) while the negative effect of SST was not as strong (-0.14 ± 0.12, Z = -1.14; Figure 4).

Regardless of model, the qualitative values of all parameters in the top models were consistent and were reflected in the model averaged parameter estimates (Table 11). AGMT had the strongest effect with a significant gain followed by a significant loss after some threshold temperature is reached. Local Kent Island temperature increases had a positive effect on hatching success (Figure 3), while increasing summer SST had the opposite effect (Figure 4). In every model, Breeding Experience had a positive effect on hatching success (Table 11).

Final analyses – interactions

We used the best model (Global + Local [+ Intrinsic]) to further investigate whether Breeding Experience interacted with temperature. Thus, we constructed three models that explored different combinations of interactions of Breeding Experience within the best model (Table 12). We compared all of these to the original best model to see if adding interactions improved our understanding of climate on hatching success.

The model that included an interaction with AGMT (both quadratic terms) was a clear improvement over the original best model without interactions (dAICc = 4.78) and somewhat better than all other models with interactions (Table 12). In this model, the overall effect of Annual Global Mean Temperature remained strong (Table 13), but the overall effect was such that hatching success of inexperienced birds increased at a greater rate with warming temperatures than hatching success of more experienced birds and also decreased at a faster rate once the inflection point was reached (Figure 5). In other words, older more experienced birds were more buffered against the impacts of temperature variation than were younger inexperienced birds.

Post-hoc analyses

Given the quadratic nature of storm-petrel response to AGMT, we wanted to gauge at what point in time the normalized global temperature crossed the temperature at which reproductive success declined (0.41; Figure 6). We calculated the least-squares estimate of normalized global temperature against Years from 1955–2010. We then identified the year at which the least-squares estimate of AGMT exceeded the tipping point identified in the final analysis. That year was 1988.

DISCUSSION

The quadratic form of the Annual Global Mean Temperature is the single most important predictor of hatching success in Leach's storm-petrels over the 56 years covered in this study. The future is not bright for this marine vertebrate breeding in the Bay of Fundy, as hatching success increased with AGMT only up to a point— 0.41 normalized °C, reached in 1988— beyond which hatching success declined as AGMT continued to rise. Since 1988, AGMT dipped below that value only eight times and it has exceeded that value every year since 2001. Projections vary for AGMT (IPCC, 2014), but no projection has AGMT dropping below this apparent critical temperature for Leach's storm-petrels in any foreseeable future.

Comparing across analyses, every model that included AGMT was far stronger than any model without AGMT. Alone, it explains most of the temperature-based variation in reproductive success of these marine vertebrates from 1955 to 2010. Although local and regional temperatures, when combined with AGMT, helped explain variation in hatching success, only AGMT consistently had Z values exceeding |2.0| in every model. The model with AGMT as the only climate predictor was nearly as useful (dAICc = 1.22) as the best model which contained both AGMT and local air temperature during the breeding season; models containing only local temperature or regional temperature were of relatively little utility (dAICc > 13) compared to any model of storm-petrel reproductive success that contained AGMT. The dominance of AGMT also was reflected in the parameter weights and the model averaged parameters. Although AGMT alone explained most of the variation in climate-related variation in hatching success, local air temperatures and SST did have appreciable effects. In fact, two models without AGMT (Local; Local + SST) demonstrated an effect of warming temperatures (i.e., $AIC_{intrinsic} - AIC_{local} > 10$) on storm-petrel reproduction. Local air temperatures at Kent Island showed a consistently positive correlation with Hatching Success, whereas SST showed a weak negative effect. In the set of top models, local air temperatures consistently showed a strong positive effect. Every model that included local air temperature strongly improved on the Intrinsic/NULL model that accounted solely for intrinsic effects such as burrow quality, individual quality, and breeding experience, but the same was not true for SST. Although the effect of SST was generally negative, in no individual model did SST show a strong effect (|Z| > 2.0) on hatching success.

Annual Global Mean Temperature is a combination of air and sea temperatures and, therefore integrates the two, perhaps encapsulating the conflicting effects of each on seabird reproductive success in the mid- to high-latitudes. It may be that the strong positive local effect of rising temperature initially outweighs any negative effects of regional SST or other unmeasured factors. At some point, local benefits are outweighed by the accumulating more general negative effects. This dynamic is best captured by the quadratic form of AGMT than by either local air temperatures or regional sea temperatures, or both in combination.

The role of air temperature on seabird survival and reproduction has been studied primarily with regard to temperature's effect on the extent of sea ice and the thereby on prey quality and abundance (Sydeman *et al.*, 2012, Sydeman *et al.*, 2015). More direct consequences of warming air temperatures are not well understood; both warmer (Sherley *et al.*, 2012) and cooler (Boersma & Rebstock, 2014) temperatures have been linked to negative effects on adult seabirds and growing chicks (rev. in Sydeman *et al.*, 2012), as well as on pinniped pups (McDonald *et al.*, 2012). In the case of Leach's storm-petrels, the positive effect of local air temperature on hatching success is probably a function of breeding in northern latitudes where warmer local air temperatures should reduce thermoregulatory costs for incubating adults.

During incubation bouts, adult Leach's storm-petrels spend extended periods of time fasting while incubating a single large egg in an underground burrow (Huntington *et al.*, 1996). Burrow temperatures are well below the thermo-neutral zone for storm-petrels (Ochoa-Acuña & Montevecchi, 2002) and highly correlated with outside air temperature (O'Connell *et al.*, 2013). Conway and Martin (2000) characterized avian incubation as a trade-off between the energetic demands of the parent and the thermal needs of the embryo. As local air temperatures increase, thermoregulatory costs to incubating adults decrease. Even small changes in the thermal environment of the nesting burrow may have large accumulated effects on incubating adults over a 44-day incubation period. Thus, it is not surprising that the direct effect of local air temperature within the context of AGMT should be strongly positive.

The effect of increasing SST was not as clear or as strong as the positive effect of local air temperature. Over the last 40 years, the net increase in SST in the Gulf of Maine, a primary foraging ground for storm-petrels breeding at Kent Island, is consistent with the global mean rate of SST warming (Balch *et al.*, 2012). Variation in Gulf of Maine SST has been linked to changes in seabird populations through changes in food availability and food quality (Diamond & Devlin, 2003) paralleled by marked changes in fisheries (Pershing *et al.*, 2015). Given these conditions, a negative effect of SST on storm-petrel reproductive success was expected. However, the response was much weaker than seen in other seabird studies (rev. in Sydeman *et al.*, 2015), perhaps because it is somewhat masked by its correlation with both local air temperatures and global temperatures.

Seabird populations are conducive to following known individuals over many years, and thus our work with storm-petrels joins previous work on blue-footed boobies *Sula nebouxii* (Oro *et al.*, 2010) and black-browed albatrosses *Thalassarche melanophris* (Nevoux *et al.*, 2010) in finding that climate change is more likely to affect inexperienced breeders than experienced breeders. In our study, the quadratic effect of AGMT is present in all age classes, but hatching success of inexperienced storm-petrels increases more rapidly than does that of experienced breeders, then declines more rapidly than that of experienced birds. It may be that the positive effect of warming local air temperature is a simple matter of physiology affecting all ages equally, but foraging ability increases with experience. Thus, with rising temperatures, inexperienced breeders may have difficulty finding food, but are compensated by lower metabolic costs while on the egg. Experienced foragers might have less need of the compensation if they arrive back at the nest with greater energetic reserves than do inexperienced individuals. The role of breeding experience in the Intrinsic model was anticipated based on prior work in this population (Mauck *et al.*, 2012), however, the interaction of breeding experience with AGMT further demonstrates the demographic complexity of responses to our changing climate.

Annual Global Mean Temperature, a metric appealing in its simplicity, is clearly the best predictor of storm-petrel response to our changing climate. Climate is more complex than simple temperature (Harley *et al.*, 2006), but temperatures are good indices of the complex changes in climate (Braganza *et al.*, 2004). At least in the case of Leach's storm-petrels breeding in the western North Atlantic, Annual Global Mean Temperature best captures the complexity faced by these seabirds over a half century of climate change.

ACKNOWLEDGEMENTS

In Memory of Charles E. Huntington (1921–2017). We thank Petra Quillfeldt and Juan F. Masello for valuable discussions during analysis and Andre Dhondt for suggestions on interpretation. We thank Eric Post for useful comments on a late draft. We thank Susie Mauck for statistical advice and general discussion. CEH and RAM thank 56 years of field assistants. RAM was supported by the Max Planck Institute for Ornithology at Radolzell while preparing this manuscript. Discussion with Jesko Parnacke's research group at the MPIO provided particularly valuable feedback. RAM was supported by a Newton Chun Award from Kenyon College. Some data were collected under NSF grant #0516784. This is contribution #265 from the Bowdoin Scientific Station at Kent Island.

REFERENCES

Balch W, Drapeau D, Bowler B, Huntington T (2012) Step-changes in the physical, chemical and biological characteristics of the Gulf of Maine, as documented by the GNATS time series. Marine Ecology Progress Series*,* **450**, 11-35.

Barbraud C (2000) Natural selection on body size traits in a long-lived bird, the snow petrel *Pagodroma nivea*. Journal of Evolutionary Biology*,* **13**, 81-88.

Bates D, Maechler M, Bolker B (2011) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-42,

Boersma PD, Rebstock GA (2014) Climate Change Increases Reproductive Failure in Magellanic Penguins. Plos One*,* **9**, e85602.

Braganza K, Karoly DJ, Arblaster JM (2004) Diurnal temperature range as an index of global climate change during the twentieth century. Geophysical Research Letters*,* **31**, 10.1029/2004gl019998.

Bunce A, Ward SJ, Norman FI (2005) Are age-related variations in breeding performance greatest when food availability is limited? Journal of Zoology*,* **266**, 163-169.

Burnham KP, Anderson DR, Burnham KP (2002) *Model selection and multimodel inference : a practical information-theoretic approach,* New York, Springer.

Burthe S, Daunt F, Butler A *et al.* (2012) Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. Marine Ecology Progress Series*,* **454**, 119-133.

Bussiere EMS, Underhill LG, Altwegg R (2015) Patterns of bird migration phenology in South Africa suggest northern hemisphere climate as the most consistent driver of change. Global Change Biology*,* **21**, 2179-2190.

Chambers LE, Altwegg R, Barbraud C *et al.* (2013) Phenological Changes in the Southern Hemisphere. Plos One*,* **8**, e.0075514.

Conway CJ, Martin T (2000) Effects of ambient temperature on avian incubation behavior. Behavioral Ecology*,* **11**, 1778-1188.

Croxall J, Trathan P, Murphy E (2002) Environmental change and Antarctic seabird populations. Science*,* **297**, 1510-1514.

Cubaynes S, Doherty PF, Schreiber EA, Gimenez O (2011) To breed or not to breed: a seabird's response to extreme climatic events. Biology Letters*,* **7**, 303-306.

Cunningham DM, Moors PJ (1994) The decline of Rockhopper Penguins *Eudyptes chrysocome* at Campbell Island, Southern Ocean and the influence of rising sea temperatures. EMU*,* **94**, 27-36.

Cunningham RM (1998) Fog studies in the Bay of Fundy over a span of 60 years. Proceedings of the First International Conference on Fog and Fog Collection, Vancouver, BC

Dearborn DC, Anders AD, Schreiber EA, Adams RMM, Mueller UG (2003) Inter-island movements and population differentiation in a pelagic seabird. Molecular Ecology*,* **12**, 2835-2843.

Dearborn DC, Gager AB, Gilmour ME, Mcarthur AG, Hinerfeld DA, Mauck RA (2015) Non-neutral evolution and reciprocal monophyly of two expressed Mhc class II B genes in Leach's storm-petrel. Immunogenetics*,* **67**, 111-123.

Diamond A, Devlin C (2003) Seabirds as indicators of changes in marine ecosystems: Ecological monitoring on Machias Seal Island. Environmental Monitoring and Assessment*,* **88**, 153-175.

Dyrcz A, Halupka L (2008) The response of the Great Reed Warbler *Acrocephalus arundinaceus* to climate change. Journal of Ornithology, **150**, 39.

Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. Proceedings of the National Academy of Sciences of the United States of America, **107**, 2078-2081.

Fagundes AI, Ramos JA, Ramos U, Medeiros R, Paiva VH (2016) Breeding biology of a winter-breeding procellariiform in the North Atlantic, the Macaronesian shearwater *Puffinus lherminieri baroli*. Zoology, **119**, 421-429.

Fay R, Barbraud C, Delord K, Weimerskirch H (2017) Contrasting effects of climate and population density over time and life stages in a long-lived seabird. Functional Ecology, **31**, 1275-1284.

Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. Science, **296**, 1689-1691.

Fox J, Hong J (2009) Effect Displays in R for Multinomial and Proportional-Odds Logit Models: Extensions to the effects Package. Journal of Statistical Software, **32**, 1-24.

Frederiksen M, Harris MP, Daunt F, Rotheryw P, Wanless S (2004) Scale-dependent climate signals drive breeding phenology of three seabird species. Global Change Biology, **10**, 1214-1222.

Fricke EC, Blizzard KM, Gannon DP, Mauck RA (2015) Model of burrow selection predicts pattern of burrow switching by Leach's Storm-Petrels. Journal of Field Ornithology, **86**, 326-336.

Friedland KD, Stock C, Drinkwater KF *et al.* (2012) Pathways between Primary Production and Fisheries Yields of Large Marine Ecosystems. Plos One, **7**, e28945.

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology, **24**, 699-711.

Hansen J, Sato M, Ruedy R, Lo K, Lea DW, Medina-Elizade M (2006) Global temperature change. Proceedings of the National Academy of Sciences of the United States of America, **103**, 14288-14293.

Harley CDG, Hughes AR, Hultgren KM *et al.* (2006) The impacts of climate change in coastal marine systems. Ecology Letters, **9**, 228-241.

Hart LA, Downs CT, Brown M (2016) Sitting in the sun: Nest microhabitat affects incubation temperatures in seabirds. Journal of Thermal Biology, **60**, 149-154.

Hervé M (2017) RVAideMemoire: Diverse Basic Statistical and Graphical Functions, https://CRAN.R-project.org/package=RVAideMemoire.

Hunt G, Coyle K, Eisner L, Edward V. Farley RaH, Franz Mueter, Jeffrey M. Napp, James E. Overland, Patrick H. Ressler, Sigrid Salo, and Phyllis J. Stabeno (2011) Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES Journal of Marine Science, **68**, 1230-1243.

Huntington CE, Butler R, Mauck RA (1996) Leach's Storm-Petrel (*Oceanodroma leucorhoa*). In: *Birds of North America.* (eds Poole A, Gill F) The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists Union, Washington, D.C.

IPCC (2013) Climate Change The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (eds Stocker T, Qin D, Plattner G-K, Tignor M, Allen S, Boschung J, Nauels A, Xia Y, Bex V, Midgley P) pp Page, Cambridge, United Kingdom and New York, NY, USA.

IPCC (2014) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (ed [Field CB, V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. Maccracken, P.R. Mastrandrea, and L.L. White) pp Page, Cambridge, UK and New York, NY, USA,, Cambridge University Press.

Kawaguchi S, Ishida A, King R *et al.* (2013) Risk maps for Antarctic krill under projected Southern Ocean acidification. Nature Climate Change, **3**, 10.1038/Nclimate1937.

Lebreton J-D (2011) The impact of global change on terrestrial Vertebrates. Comptes Rendus Biologies, **334**, 360-369.

Lucey SM, Nye JA (2010) Shifting species assemblages in the Northeast US Continental Shelf Large Marine Ecosystem. Marine Ecology Progress Series, **415**, 23-33.

Maas CJM, Hox JJ (2005) Sufficient Sample Sizes for Multilevel Modeling. Methodology, **1**, 86-92.

Mackas D, Batten S, Trudel M (2007) Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. Progress in Oceanography, **75**, 223-252.

Mauck R, Huntington C, Grubb T (2004) Age-specific reproductive success: Evidence for the selection hypothesis. Evolution, **58**, 880-885.

Mauck RA, Adrianowycz SA, Mcmahon C, Acker H, Taylor L, Dearborn DC (2016) Sex-specific foraging behavior during the incubation period in Leach's storm-petrels. 6th International Albatross and Petrel Conference, Barcelona, Spain

Mauck RA, Huntington CE, Doherty Jr PF (2012) Experience versus effort: what explains dynamic heterogeneity with respect to age? Oikos, **121**, 1379-1390.

Mauck RA, Ricklefs RE (2005) Control of fledging age in Leach's Storm-Petrel, *Oceanodroma leucorhoa*: chick development and prefledging mass loss. Functional Ecology*,* **19**, 73-80.

Mauck RA, Waite TA, Parker PG (1995) Monogamy in Leach's Storm-Petrel: DNA-fingerprinting evidence. AUK*,* **112**, 473-482.

Mauck RA, Zangmeister JL, Cerchiara JC, Huntington CE, Haussmann MF (2011) Male-biased reproductive effort in a long-lived seabird. Evolutionary Ecology Research*,* **13**, 19-33.

Mcdonald BI, Goebel ME, Crocker DE, Costa DP (2012) Biological and Environmental Drivers of Energy Allocation in a Dependent Mammal, the Antarctic Fur Seal Pup. Physiological and Biochemical Zoology*,* **85**, 134-147.

Nevoux M, Forcada J, Barbraud C, Croxall J, Weimerskirch H (2010) Bet-hedging response to environmental variability, an intraspecific comparison. Ecology*,* **91**, 2416-2427.

Nye J, Link J, Hare… J (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series*,* **393**, 111-129.

O'brien RM (2007) A caution regarding rules of thumb for variance inflation factors. Quality & Quantity*,* **41**, 673-690.

O'connell C, Villar-Leeman C, Fricke E, Gannon D, Mauck R (2013) The heat is on: air temperature, burrow temperature, and reproductive success in a long-lived seabird. Society for Integrative and Comparative Biology, San Francisco

Ochoa-Acuña H, Montevecchi W (2002) Basal metabolic rate of adult Leach’s storm-petrels during incubation. Waterbirds*,* **25**, 249-252.

Olsen P, Baker GB (2001) Daytime incubation temperatures in nests of the Nankeen Kestrel, Falco cenchroides. EMU, **101**, 255-258.

Oro D, Torres R, Rodriguez C, Drummond H (2010) Climatic influence on demographic parameters of a tropical seabird varies with age and sex. Ecology, **91**, 1205-1214.

Pardo D, Jenouvrier S, Weimerskirch H, Barbraud C (2017) Effect of extreme sea surface temperature events on the demography of an age-structured albatross population. Philosophical Transactions of the Royal Society B-Biological Sciences, **372**.

Perez EA, Marco A, Martins S, Hawkes LA (2016) Is this what a climate change-resilient population of marine turtles looks like? Biological Conservation, **193**, 124-132.

Pershing AJ, Alexander MA, Hernandez CM *et al.* (2015) Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science, **350**, 809-812.

Pollard E, Moss D (1995) Historical Records of the Occurrence of Butterflies in Britain - Examples Showing Associations between Annual Number of Records and Weather. Global Change Biology, **1**, 107-113.

Pollet IL, Hedd A, Taylor PD, Montevecchi WA, Shutler D (2014) Migratory movements and wintering areas of Leach's Storm-Petrels tracked using geolocators. Journal of Field Ornithology, **85**, 321-328.

Rayner NA, Parker DE, Horton EB *et al.* (2003) Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. Journal of Geophysical Research-Atmospheres, **108**.

Ricklefs RE, Roby, D.D. Williams, J.B (1986) Daily energy expenditure by adult Leach's storm-petrels during the nesting cycle. Physiological Zoology, **59**, 649-660.

Rolland V, Weimerskirch H, Barbraud C (2010) Relative influence of fisheries and climate on the demography of four albatross species. Global Change Biology, **16**, 1910-1922.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature, **421**, 57-60.

Rosenzweig C, Karoly D, Vicarelli M *et al.* (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature, **453**, 353-U320.

Saba VS, Stock CA, Spotila JR, Paladino FV, Tomillo PS (2012) Projected response of an endangered marine turtle population to climate change. Nature Climate Change, **2**, 814-820.

Sandvik H, Erikstad K, Saether B-E (2012) Climate affects seabird population dynamics both via reproduction and adult survival. Marine Ecology-Progress Series, **454**, 273-284.

Santisteban L, Benkman C, Fetz T, Smith J (2012) Survival and population size of a resident bird species are declining as temperature increases. Journal of Animal Ecology, **81**, 352-363.

Schreiber E, Burger J (2002) Seabirds in the Marine Environment. In: *Biology of Marine Birds.* (eds Schreiber E, Burger J) pp Page. Boca Raton, CRC Press.

Sherley RB, Ludynia K, Underhill LG, Jones R, Kemper J (2012) Storms and heat limit the nest success of Bank Cormorants: implications of future climate change for a surface-nesting seabird in southern Africa. Journal of Ornithology, **153**, 441-455.

Shoji A, Yoneda M, Gaston A (2012) Ocean climate variability links incubation behaviour and fitness in Ancient Murrelets (*Synthliboramphus antiquus*). Canadian Journal of Zoology-Revue Canadienne De Zoologie, **90**, 361-367.

Sydeman W, Thompson S, Kitaysky A (2012) Seabirds and climate change: roadmap for the future. Marine Ecology-Progress Series, **454**, 107-117.

Sydeman WJ, Poloczanska E, Reed TE, Thompson SA (2015) Climate change and marine vertebrates. Science, **350**, 772-777.

Sydeman WJ, Thompson SA, Piatt JF *et al.* (2017) Regionalizing indicators for marine ecosystems: Bering Sea-Aleutian Island seabirds, climate, and competitors. Ecological Indicators, **78**, 458-469.

Team RC (2015) R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria,

Tomillo PS, Oro D, Paladino FV, Piedra R, Stieg AE, Spotila JR (2014) High beach temperatures increased female-biased primary sex ratios but reduced output of female hatchlings in the leatherback turtle. Bological Conservation, **176**, 71-79.

Valtonen A, Leinonen R, Poyry J, Roininen H, Tuomela J, Ayres MP (2014) Is climate warming more consequential towards poles? The phenology of Lepidoptera in Finland. Global Change Biology, **20**, 16-27.

Weimerskirch H (1990) Weight loss of Antarctic fulmars - *Fulmarus-glacialoides* - during incubation and chick brooding. Ibis, **132**, 68-77.

Weimerskirch H, Louzao M, De Grissac S, Delord K (2012) Changes in Wind Pattern Alter Albatross Distribution and Life-History Traits. Science, **335**, 211-214.

Zangmeister JL, Haussmann MF, Cerchiara J, Mauck RA (2009) Incubation failure and nest abandonment by Leach's Storm-Petrels detected using PIT tags and temperature loggers. Journal of Field Ornithology, **80**, 373-379.

TABLES

Table 1. Distribution of raw values for climate variables used in analyses. AGMT = Annual Global Mean Temperature (°C relative to reference value), BGMT = Breeding Season (May, June, July) Global Mean Temperature (°C relative to reference value), SST_b = Breeding Season Sea Surface Temperatures (°C), SST_w = Winter (December, January, February) Sea Surface Temperatures (°C), Local = Mean air Temperature (°C) at Kent Island. N = 56 years.

Var	mean	sd	min	max	skew	kurtosis
AGMT	0.3	0.3	-0.2	0.7	0.2	-1.2
BGMT	0.2	0.2	-0.2	0.7	0.3	-1.1
SST_b	13.1	0.7	11.4	14.7	-0.2	-0.1
SST_w	26.0	0.3	25.5	26.7	0.2	-0.5
Local	13.1	0.7	11.2	14.4	-0.3	-0.3

Table 2. Correlation among climate variables that served as a basis for the initial screening of variables across N = 56 years.

Variable	AGMT	BGMT	SSTsu	SSTw
BGMT	0.99			
SST$_b$	0.43	0.44		
SST$_w$	0.53	0.52	0.07	
Local	0.68	0.69	0.76	0.28

Table 3. Intrinsic candidate models. Models of Hatching Success without climate variables. Model = fixed effects in the model. BE = breeding experience (years), PBLen = pairbond length (years), NULL = no fixed effects. #Par = parameters in model equal to fixed effects + intercept + random effects (Year, Individual ID, Pairbond ID, Burrow ID). AIC = Akaike's Information Criterion. AICc = AIC adjusted for sample size. dAICc = difference between model AICc and the lowest AICc among all candidate models. *w* = Akaike weight. Cum Rank = the accumulated model weight within the model set. Observations = 24,198, Individuals = 5287, Pairs = 4430; Burrows = 1278; Years = 56. Bold denotes fixed effects retained in the Intrinsic model.

Model	#Par	AIC	AICc	dAICc	*w*	Cum Rank
BE	5	19800	19800.11	0.00	0.625	0.625
PBLen + BE	6	19801	19801.13	1.03	0.374	0.998
NULL	4	19813	19813.08	12.98	0.001	0.999
PBLen	5	19814	19814.11	14.00	0.001	1.000

Table 4. Hatching success models with variations on Global Temperature. Model = climate-related fixed effects in the model. AGMT = Annual Global Mean Temperature, BGMT = Breeding Season (May, June, July) Global Mean Temperature , 5-Yr AGMT = running 5-year average of AGMT. #Par = parameters in model equal to climate-related fixed effects + breeding experience (fixed effect) + random effects (Year, Individual ID, Pairbond ID, Burrow ID). AIC = Akaike's Information Criterion. AICc = AIC adjusted for sample size. dAICc = difference between model AICc and the lowest AICc among all candidate models. *w* = Akaike weight. Cum Rank = the accumulated model weight within the model set. Observations = 25,879, Individuals = 5855, Pairs = 5357; Burrows = 1435; Years = 56. Bold denotes fixed effects represented by the variable AGMT in the final analyses.

Model	#Par	AIC	AICc	dAIC	*w*	Cum Rank
AGMT + AGMT^2	7	22002.2	22002.33	0.00	0.800	0.800
BGMT + BGMT^2	7	22005.0	22005.15	2.82	0.195	0.995
BGMT	6	22014.2	22014.29	11.95	0.002	0.998
AGMT	6	22015.1	22015.16	12.82	0.001	0.999
5-Yr AGMT	6	22015.3	22015.45	13.12	0.001	1.000
5-Yr AGMT + 5-Yr^2	7	22023.3	22023.45	21.11	0.000	1.000

Table 5. Hatching Success Models with variations on Regional Sea Surface Temperatures. Model = climate-related fixed effects in the model. SST_b = Breeding Season Sea Surface Temperatures, SST_w = Winter (December, January, February) Sea Surface Temperatures. #Par = parameters in model equal to fixed effects + breeding experience (fixed effect) + random effects (Year, Individual ID, Pairbond ID, Burrow ID). AIC = Akaike's Information Criterion. AICc = AIC adjusted for sample size. dAICc = difference between model AICc and the lowest AICc among all candidate models. *w* = Akaike weight. Cum Rank = the accumulated model weight within the model set. Observations = 25,879, Individuals = 5855, Pairs = 5357; Burrows = 1435; Years = 56. Bold denotes fixed effects represented by the variable S in the final analyses.

Model	#Par	AIC	AICc	dAICc	*w*	Cum Rank
$\mathbf{SST_b}$	6	22023.6	22023.71	0.00	0.652	0.652
$SST_b + SST_b^2$	7	22025.2	22025.33	1.63	0.289	0.941
SST_w	6	22029.1	22029.21	5.50	0.042	0.982
$SST_w + SST_w^2$	7	22030.8	22030.93	7.23	0.018	1.000

Table 6. Hatching Success Models with variations on Local Air Temperatures at Kent Island. Model = climate-related fixed effects in the model. KI = Mean daily air temperature on Kent Island during the incubation season (June, July). #Par = parameters in model equal to fixed effects + breeding experience (fixed effect) + random effects (Year, Individual ID, Pairbond ID, Burrow ID). AIC = Akaike's Information Criterion. AICc = AIC adjusted for sample size. dAICc = difference between model AICc and the lowest AICc among all candidate models. *w* = Akaike weight. Cum Rank = the accumulated model weight within the model set. Observations = 25,879, Individuals = 5855, Pairs = 5357, Burrows = 1435; Years = 56. Bold denotes fixed effects represented by the variable L in the final analyses.

Model	#Par	AIC	AICc	dAICc	*w*	Cum Rank
KI	6	22014.8	22014.91	0.00	0.714	0.714
KI + KI^2	7	22016.6	22016.73	1.83	0.286	1.000

Table 7. Hatching Success Models in the final analysis representing all possible combinations of the variables derived from the initial analyses of temperature variables. Model = climate-related fixed effects in the model. Global = Annual Mean Global Temperature quadratic form (i.e., Global stands for Global + Global2), SST = Breeding Season Sea Surface Temperature, Local = Kent Island Mean Daily Air Temperature during the breeding season. #Par = parameters in model equal to fixed effects + age + random effects (Year, Individual ID, Pairbond ID, Burrow ID). AIC = Akaike's Information Criterion. AICc = AIC adjusted for sample size. dAICc = difference between model AICc and the lowest AICc among all candidate models. *w* = Akaike weight. Cum Rank = the accumulated model weight within the model set. Observations = 25,879, Individuals = 5855, Pairs = 5357; Burrows = 1435; Years = 56.

Model	#Par	AIC	AICc	dAIC	*w*	Cum Rank
Global + Local	8	22001.0	22001.11	0.00	0.408	0.408
Global + Local + SST	9	22001.6	22001.83	0.72	0.284	0.692
Global	7	22002.2	22002.33	1.22	0.221	0.913
Global + SST	8	22004.1	22004.21	3.10	0.087	0.999
Local	6	22014.9	22014.96	13.84	0.000	1.000
Local + SST	7	22016.5	22016.61	15.50	0.000	1.000
SST	6	22023.9	22024.01	22.89	0.000	1.000
Intrinsic	5	22026.8	22026.92	25.81	0.000	1.000

Table 8. Parameter Weights for each category of climate variable in the final analysis. Global = Global Temperature, SST = Breeding Season Sea Surface Temperature, Local = Mean Daily Kent Island Air Temperature. Parameter weight is calculated after Burnham and Anderson (2002) and reflects the relative value of every model in which that parameter appears in the candidate models (from Table 7).

Variable	Wt.
Global	1.00
Local	0.69
SST	0.37

Table 9. Fixed effects for the Full model in the final analysis. BE = Breeding Experience, Global = Global Temperature, SST = Breeding Season Sea Surface Temperature, Local = Mean Daily Kent Island Air Temperature.

	Estimate	SE	Z
(Intercept)	2.03	0.16	12.81
BE	0.13	0.03	3.70
Local	0.29	0.14	2.12
SST	-0.14	0.12	-1.14
Global	0.29	0.12	2.51
Global ^{2}	-0.37	0.09	-3.94

Table 10. Fixed effects for the best model in the final analysis. BE = Breeding Experience, Global = Global Temperature, Local = Mean Daily Kent Island Air Temperature.

Effect	Estimate	SE	Z
(Intercept)	2.02	0.16	12.76
BE	0.13	0.03	3.71
Local	0.18	0.10	1.83
Global	0.31	0.12	2.63
Global ^{2}	-0.35	0.09	-3.79

Table 11. Model averaged parameter estimates. Method for estimation is in parentheses.

	BE	Global	$Global^2$	Local	SST
Mean (ZERO)	0.129	0.340	-0.356	0.155	-0.036
SE	0.007	0.090	0.057	0.078	0.121
Mean (NAT)	0.129	0.340	-0.356	0.505	-0.096
SE	0.008	0.016	0.021	0.004	0.021

Table 12. Best Hatching Success Model with all possible interactions between climate variable and the fixed effect of Breeding Experience. Interactors = variables interacting with Breeding Experience. Global = Annual Mean Global Temperature Anomaly quadratic form (i.e., Global stands for Global + Global2), Local = Kent Island Mean Daily Air Temperature during the breeding season. #Par = parameters in model equal to fixed effects + age + random effects (Year, Individual ID, Pairbond ID, Burrow ID). AIC = Akaike's Information Criterion. AICc = AIC adjusted for sample size. dAICc = difference between model AICc and the lowest AICc among all candidate models. w = Akaike weight. Cum Rank = the accumulated model weight within the model set. Observations = 25,879, Individuals = 5855, Pairs = 5357; Burrows = 1435; Years = 56.

Interactors	#Par	AIC	AICc	dAIC	*w*	Cum Rank
Global	10	21996.1	21996.33	0.00	0.515	0.515
Global + Local	11	21997.4	21997.67	1.34	0.264	0.778
Local	9	21998.3	21998.49	2.16	0.174	0.953
Full w/o interactions	8	22001.0	22001.11	4.78	0.047	1.000

Table 13. Summary of fixed effects for best model of Hatching Success with interactions. BE = Breeding Experience, Global = Global Temperature Anomaly, Local = Kent Island Temperature.

	Estimate	SE	Z
(Intercept)	2.14	0.17	12.38
BE	0.07	0.05	1.63
Local	0.18	0.10	1.90
Global	0.52	0.15	3.55
Global^2	-0.50	0.14	-3.66
BE*Global	-0.10	0.04	-2.49
BE*Global^2	0.08	0.04	1.80

FIGURE CAPTIONS

Figure 1. Raw values for base climate variables from 1955-2010. a = Annual Mean Global Temperature (°C relative to reference value). b = Sea Surface Temperature (°C) during the breeding season in the Gulf of Maine/Georges Banks. c = Local (Kent Island) air temperatures (°C) during May, June, and July.

Figure 2. The adjusted Effect of Annual Global Mean Temperature on Hatching Success on Kent Island from 1955– 2010. The solid line represents the adjusted effect of Global Temperature from the Full Model. The shaded area represents the 95% confidence interval of the estimate. Global Temperatures are normalized. Hatching success is on the logit scale. Tick marks above the x-axis denote values represented during the period of study.

Figure 3. The adjusted Effect of Local (Kent Island) Air Temperature on Hatching Success on Kent Island from 1955–2010. Based on the Full Model. Temperatures are normalized. Hatching success is on the logit scale. The solid line represents the adjusted effect of Local Air Temperature from the Full Model. The shaded area represents the 95% confidence interval of the estimate. Tick marks above the x-axis denote values represented during the period of study.

Figure 4. The adjusted Effect of Sea Surface Temperature in the Gulf of Maine/ Georges Banks during the incubation period (May, June, July) from 1955– 2010. Based on the Full Model. Sea Surface Temperatures are normalized. Hatching success is on the logit scale. The solid line represents the adjusted effect of SST from the Full Model. The shaded area represents the 95%

confidence interval of the estimate. Tick marks above the x-axis denote values represented during the period of study.

Figure 5. Interaction of Breeding Experience and Annual Global Mean Temperature on Hatching Success on Kent Island from 1955– 2010. Three age classes after Mauck et al. (2012) that increase from left to right. a = individuals in their first year of breeding on Kent Island. b = all individuals in their second year of breeding on Kent Island. c = all individuals with three or more years of breeding experience. Global Temperature values are normalized. Hatching success is on the logit scale. Tick marks above the x-axis denote values represented during the period of study. The solid lines represent adjusted effect of Global Temperature from the best interaction model (Tables 12, 13). The shaded area represents the 95% confidence interval of the estimates.

Figure 6. The Tipping Point. a) Normalized AGMT at which hatching success begins to decline (0.41). b) Dashed line represents the least-squares relationship between AGMT and Year (1955–2010). The year (1988) at which the least squares line crossed 0.41.