

present in southern China<sup>22</sup>, our age estimate provides evidence for the oldest known artifact assemblage consisting of indisputable tool forms in east Asia. It also denotes the oldest unambiguous presence of early humans in east Asia at a latitude of at least 40°N, following the range extension to this same latitude in western Eurasia by about 1.7 Myr<sup>3</sup>. The spread of toolmakers to this latitude implies that early Pleistocene human populations in east Asia were able to adapt to diverse climatic settings. It also suggests that populations might have dispersed to and from east Asia over a broad latitudinal range, although highlands of the Qinghai–Tibetan Plateau probably limited a northern migration route. The age of the XCL Palaeolithic site is, furthermore, about 0.2 Myr earlier than *Homo erectus* (about 1.15 Myr) found at Lantian<sup>23</sup>, located on the middle Yellow River, roughly 900 km southwest of the Nihewan Basin (Fig. 1). These two localities suggest that populations were able to occupy or shift their range over a considerable area, from Nihewan to the southern margin of the Loess Plateau, during a time of enhanced global and regional climatic variability that included intermittent aridification of north China<sup>24,25</sup>. □

## Methods

### Rock magnetic methods and results

Stepwise acquisition of isothermal remanent magnetization was investigated using an alternating gradient field magnetometer up to 2.2 T and pulse magnetometer up to 2.7 T. For 95% of the samples studied, 90% of the saturation magnetization was acquired below 0.3 T, showing that a low-coercivity magnetic carrier dominates the remanence. After removing the coarser fraction (> 100 µm), we used thermomagnetic analysis of the bulk sediment to determine a Curie point of 580 °C, which is characteristic of pure magnetite. The saturation magnetization ( $M_s$ ), saturation remanence ( $M_{rs}$ ), coercivity field ( $H_c$ ) and the coercivity of the remanence ( $H_{cr}$ ) were determined and their ratios combined in a Day plot<sup>26</sup>. This plot indicates that the magnetite grain sizes are predominantly pseudo-single domain. Details of the magnetic properties of the carriers will be addressed elsewhere.

### Anisotropy of magnetic susceptibility

Anisotropy of magnetic susceptibility (AMS) measurements were performed using a Kappabridge KLY-3s (Geofyzika Brno). The susceptibility tensor for each sample was calculated from measurements in 15 positions, by a described method<sup>27</sup>. To avoid potential problems associated with heating<sup>28</sup>, we completed the AMS measurements before any thermal demagnetization was conducted. In the 666 samples studied, the magnetic lineation ( $L$ ) was found to be smaller than the magnetic foliation ( $F$ ), indicating that the AMS ellipsoid is oblate. Most minimum susceptibility axes ( $K_{min}$ ) are close to the vertical, perpendicular to the bedding plane ( $I_{mean} = 78.3^\circ$ ), and tightly grouped, whereas the inclinations of the maximum axes ( $K_{max}$ ) are very shallow ( $I_{mean} = 6.7^\circ$ ). These results are typical for an original sedimentary magnetic fabric that has been unperturbed since deposition.

### Demagnetization of the NRM

Remanence measurements were made using a 2G three-axis cryogenic magnetometer installed in field-free space (< 300 nT). We performed stepwise alternating field and thermal demagnetization techniques on 1,611 samples taken from the two sections. Both methods could isolate the characteristic remanent magnetization after removing one or two soft components of magnetization (see Supplementary Information). Total 223 (80%) and 207 (81%) sampling levels with 669 and 621 oriented samples gave reliable characteristic remanence directions at XCL and DG, respectively. NRM intensities for 669 samples at XCL range from 30.6 to 1,792 mA m<sup>-1</sup> with a mean value of 285.2 mA m<sup>-1</sup>; similarly, for 621 samples at DG the intensities range from 29.6 to 1,770 mA m<sup>-1</sup> with a mean value of 248.9 mA m<sup>-1</sup>.

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## Lagged effects of ocean climate change on fulmar population dynamics

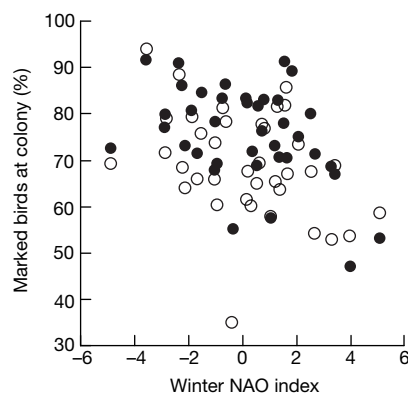
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Environmental variation reflected by the North Atlantic Oscillation affects breeding and survival in terrestrial vertebrates<sup>1,2</sup>, and climate change is predicted to have an impact on population dynamics by influencing food quality or availability<sup>3</sup>. The North Atlantic Oscillation also affects the abundance of marine fish and zooplankton<sup>4,5</sup>, but it is unclear whether this filters up trophic levels to long-lived marine top predators. Here we show by analysis of data from a 50-year study of the fulmar that two different indices of ocean climate variation may have lagged effects on population dynamics in this procellariiform seabird.

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**Figure 1** Annual variation in the percentage of colour-ringed adult fulmars that were observed at the colony during each breeding season in relation to the annual North Atlantic Oscillation index for that summer. Data are presented separately for males (filled

circles) and females (open circles). All adults used in the analysis were known to have bred and were later confirmed to be alive in that season.

**Annual variability in breeding performance is influenced by the North Atlantic Oscillation, whereas cohort differences in recruitment are related to temperature changes in the summer growing season in the year of birth. Because fulmars exhibit delayed reproduction, there is a 5-year lag in the population's response to these effects of environmental change. These data show how interactions between different climatic factors result in complex dynamics, and that the effects of climate change may take many years to become apparent in long-lived marine top predators.**

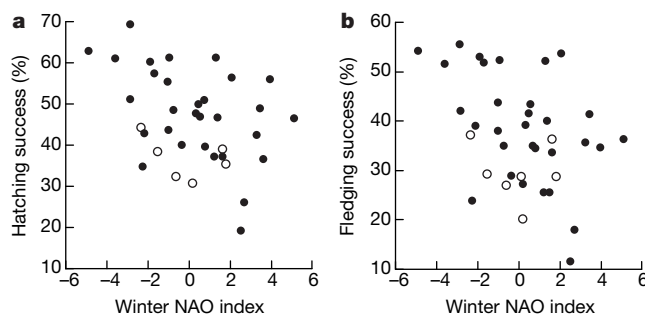
The northern fulmar, *Fulmarus glacialis*, is one of the most abundant seabirds in the North Atlantic and has provided a classic example of species range expansion in the past two centuries<sup>6</sup>. Although some think that this expansion may have resulted from increased discards from whaling and fishing activities<sup>7</sup>, others have argued that the pattern of expansion is better explained by oceanographic changes<sup>8,9</sup>. Uncertainty over the foraging areas used by birds from different breeding colonies has prevented explicit tests of these hypotheses<sup>9,10</sup>. Furthermore, environmental variability is most likely to affect reproductive success<sup>11,12</sup>, or the survival of juveniles rather than adults<sup>13</sup>. Because these long-lived seabirds do not recruit to breeding colonies until they are several years old<sup>14</sup>, a time series of several decades may be required to assess the demographic consequences of the factors influencing those early life stages.

Since 1950, studies of fulmar population ecology have been made on Eynhallow, Scotland<sup>15</sup>, offering a rare opportunity to explore the effects of climate change on seabird colony dynamics. The proportion of breeding adults present at the colony each summer was related significantly to the winter North Atlantic Oscillation (NAO) index (Fig. 1) for both males (analysis of variance (ANOVA)  $F_{1,36} = 8.30$ ,  $P < 0.01$ ,  $r^2 = 0.19$ ) and females ( $F_{1,36} = 4.17$ ,  $P < 0.05$ ,  $r^2 = 0.10$ ), with the lower probability of recording females at the colony reflecting sex differences in foraging cycles<sup>14</sup>. The absence of breeding adults in any one year could result from unrecorded early nest failures or intermittent breeding<sup>16,17</sup>, either of which could be related to the NAO through its impact on secondary production in the northeast Atlantic<sup>4</sup>. Alternatively, variations in wind speed markedly affect the cost of flight in these soaring birds<sup>18</sup>, and the occurrence of weaker westerlies during a negative NAO<sup>19</sup> may simply increase the probability of birds being observed at the colony. Whatever the ultimate cause, the NAO's influence on the attendance patterns of breeding adults clearly needs to be considered when making inferences about the size of a population from a census of nesting pairs.

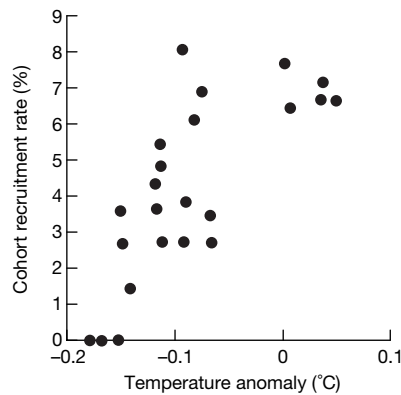
More significantly for their demography, hatching success and fledging success in the following summer were both related

significantly to the winter NAO index (hatching success,  $F_{1,34} = 5.23$ ,  $P < 0.05$ ,  $r^2 = 0.14$ , Fig. 2a; fledging success,  $F_{1,36} = 6.52$ ,  $P < 0.05$ ,  $r^2 = 0.15$ , Fig. 2b). Multivariate analyses incorporating environmental factors, density and levels of disturbance indicated that colony size did not influence these reproductive parameters; however, the winter NAO and previously reported effects of disturbance together explained almost 30% of the observed variation in annual fledging success ( $F_{2,32} = 6.92$ ,  $P < 0.01$ ,  $r^2 = 0.28$ ). The abundance of overwintering *Calanus* in the North Sea increases during negative NAO conditions<sup>4</sup>, and this may provide a link between these observed effects on reproductive success through an increase in availability of the crustaceans and fish that are known to be taken by fulmars in Scottish waters<sup>20</sup>. Alternatively, poor reproductive success may reflect the severe winter conditions experienced in low NAO years<sup>19</sup>.

Variation in the proportion of fledged chicks that subsequently recruited to the colony was investigated for cohorts born between 1958 (when long-lasting monel rings were first used) and 1980 (to allow sufficient time to detect new breeders). The proportion of each of these cohorts that returned to breed at the study colony varied markedly, with no recorded recruits from some cohorts and up to 8% in others. We then used stepwise multiple regression to determine which factors influenced this observed variation in cohort recruitment rate. There was no support for any effects of the NAO, colony size or fishing activity, but there was a significant relationship between cohort recruitment rate and summer growing season temperatures in the Northern Hemisphere (Fig. 3;  $F_{1,21} = 27.16$ ,  $P < 0.001$ ,  $r^2 = 0.56$ ), a measure that integrates large-scale variation in land and sea temperatures<sup>21</sup>.



**Figure 2** Variation in annual values for hatching success and fledging success in relation to the NAO index for the winter before the breeding season. **a**, Hatching success; **b**, fledging success. Data from years when there were high levels of disturbance through the incubation and nestling period ( $>10$  days) are represented as open circles.



**Figure 3** The recruitment rate for different cohorts of chicks from the study colony was significantly related to anomalies in Northern Hemisphere growing season temperatures during the cohort year of birth (1958–80). Recruitment rates were based on the

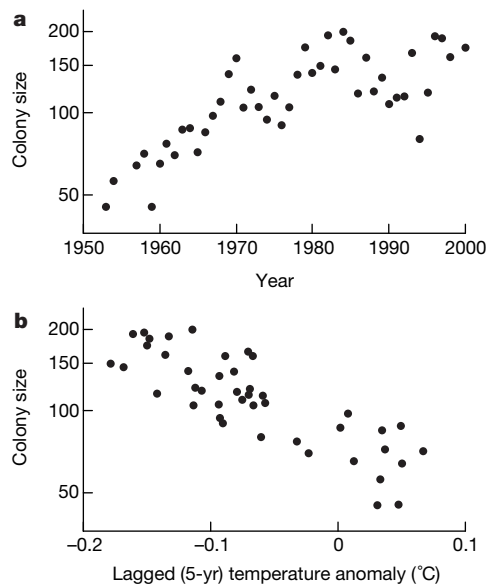
percentage of fledged chicks from the Eynhallow colony that were found breeding back at the colony within the following 18 years. Ninety per cent of all known-age recruits at the colony were first recorded breeding before they were 18 years old.

For many long-lived marine top predators of commercial or conservation interest, population trends are assessed through annual counts of occupied nest sites<sup>6</sup>, or adults present at breeding colonies<sup>22,23</sup>. These findings suggest that any effects of climate change on these indices of population size will be difficult to detect without a detailed understanding of the underlying demographic processes. Given the observed effects of the winter NAO on attendance at the colony (Fig. 1) and breeding performance (Fig. 2), and of temperature on subsequent recruitment (Fig. 3), one would predict that colony size will be influenced by a complex interaction between these different climate indices. Furthermore, many long-lived vertebrates such as fulmars do not recruit until they are several years old, and the effects of changes in breeding performance and recruitment on colony dynamics should therefore be lagged.

Annual estimates of the size of our study colony show a general increase throughout the study period, but with marked oscillations over the past 30 years (Fig. 4a). As predicted, the colony size was significantly related to the previous winter's NAO index ( $P < 0.03$ ),

and to lagged values for the winter NAO ( $P < 0.05$ ) and Northern Hemisphere summer temperatures ( $P < 0.001$ ), with a time lag of 5 years providing the overall best fit model ( $F_{5,33} = 18.02$ ,  $P < 0.001$ ,  $r^2 = 0.73$ ). However, colony sizes were greatest after periods when recruits had been born in cooler conditions (Fig. 4b), contrary to our predictions that were based on observed effects of temperature on local recruitment (Fig. 3). These data suggest that the cooler temperatures experienced by young birds could affect cohort dispersal rates rather than survival. If so, increases in colony size after these conditions may reflect an increase in recruits from the much larger colonies found in arctic areas.

Among long-lived vertebrates, the influence of environmental variation has generally been most clearly shown through effects on reproductive success<sup>11,12</sup> and early survival<sup>13</sup>. These findings illustrate how delayed maturity in these long-lived species will mean that the effects of climate change on breeding population size are likely to be lagged, with the period of lag depending on the species' life-history characteristics. Future attempts to detect the impacts of climate change must carefully consider contemporary population trends in relation to the effects of environmental variation on both survival and dispersal of these early life stages. □



**Figure 4** Variations in the number of fulmars breeding on Eynhallow. **a**, Trends in the size of the study colony (1953–2000). **b**, Changes in colony size in relation to lagged (5-year) Northern Hemisphere temperature anomalies.

## Methods

### Study colony and data collection

The study colony was located on a 1-km<sup>2</sup> uninhabited island in Orkney, Scotland (59° 8' N, 3° 8' W), where fulmars nest on rocky cliffs, derelict buildings, stone walls and low grassy cliffs. In most years between 1950 and 1995, visits were made in May (to search for occupied nest sites and record marked adults), July (to estimate hatching success) and August (to ring chicks)<sup>24</sup>. All chicks that survived to be ringed in August were considered to have fledged. Estimates of colony size were based on the number of nests containing an egg in May. Many known nest sites remained unoccupied, even in years of peak colony size, and competition for nest sites appeared unlikely to influence recruitment rates. Each year, a sample of new recruits to the breeding population were marked with individual colour-ring combinations, and their sex was determined from bill measurements<sup>25</sup>. Roughly 60% of the breeding population were marked throughout most of the study period<sup>14</sup>. Between 1996 and 2000, fewer visits were made, but these were sufficient to estimate colony size in all years except 1999, and to identify any new recruits that had been ringed as chicks.

### Climate indices

Data on Northern Hemisphere temperature anomalies were based on smoothed tree ring re-constructions<sup>21</sup>, providing a suitably large-scale proxy that integrates marine and terrestrial growing season temperatures across the fulmar's geographical range. These data are available from the website of the National Geophysical Data Centre, USA (<http://www.ngdc.noaa.gov/paleo.html>). Data on the winter North Atlantic Oscillation index<sup>26</sup> were obtained from the website of the National Centre for Atmospheric Research, Boulder, USA (<http://www.cgd.ucar.edu/cas/catalog/climind/>). The winter NAO index is an integrated measure that influences many climatic variables such as precipitation, windspeed and temperature over large parts of the Northern Hemisphere<sup>19,26</sup>. The annual Scottish Fisheries Statistics (available from Her Majesty's Stationary Office, Edinburgh)

were used to provide indices of fishing activity. These indices were based on the annual weight of landings of demersal species by Scottish boats to ports in Orkney and Shetland, and to all Scottish ports. Analyses focused on demersal catches because these fisheries were the most likely to produce by-catch and fisheries waste.

## Data analyses

Estimates of cohort variation in recruitment rate were based on the 1,281 chicks that were ringed at sites on Eynhallow between 1958 and 1980. The effort put into catching the new recruits to the breeding population varied between years, but should not bias overall estimates of cohort recruitment rate because searching effort for each cohort was integrated over 18 field seasons. The probability of observing breeding adults at the colony was estimated for colour-ringed birds that were confirmed breeders and known to be alive in that year (on the basis of positive sightings in subsequent years). Analyses were based on observations made between 1954 and 1995, using a total sample of 987 colour-ringed breeding adults.

To standardize effort across years, estimates of colony size, hatching success and fledging success excluded data from part of the colony where steep cliffs prevented easy access to nest sites. The sub-area used in this study represented roughly 64% of the whole colony, and these estimates therefore differ slightly from previously published data from all nests<sup>24</sup>. A highly significant relationship between the number of occupied nests in this sub-area and the whole colony (data from 1950 to 1995:  $F_{1,44} = 808$ ,  $P < 0.0001$ ,  $r^2 = 0.95$ ) suggests that its demographic development was representative.

Because disturbance has been shown previously to influence breeding performance<sup>27</sup>, we also incorporated this factor into our analysis of variations in reproductive success. Annual estimates of disturbance levels were based on the number of days that researchers were present on the island during the incubation and chick-rearing period. The influence of different climate indices, fishing effort and disturbance on cohort recruitment rate and breeding performance (hatching success and fledging success) was determined by stepwise multiple regression. Initial factors included in each model were (1) colony size; (2) Northern Hemisphere temperature anomaly; (3) winter NAO; (4) annual NAO; (5) year; (6) Scottish demersal catch; (7) Orkney and Shetland demersal catch; and (8) disturbance.

The demographic consequences of observed environmentally induced variation in reproductive success and recruitment were initially analysed using an autoregressive model that estimated the influence of the following variables on subsequent colony size: (1) winter NAO index (which is predicted to influence attendance; Fig. 1); (2) lagged values for colony size; and (3) lagged values for the winter NAO index (which are predicted to influence the number of fledglings produced in previous cohorts; Fig. 2b); and (4) lagged values for the Northern Hemisphere temperatures (which are predicted to influence the subsequent recruitment rate for each cohort of fledglings; Fig. 3). The effect of lagged values for colony size was not significant, and this variable was therefore dropped from the final model. Year was included in each model to account for the strong temporal trend in the data. Values of 1–9 years were used for the time lag in the effects of colony size and climate indices on future colony size, on the basis of biologically reasonable estimates of the delay between fledging and first reproduction<sup>14</sup>.

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# Histamine regulates T-cell and antibody responses by differential expression of H1 and H2 receptors

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Many pathological processes, including those causing allergies and autoimmune diseases, are associated with the presence of specialized subsets of T helper cells ( $T_H1$  and  $T_H2$ ) at the site of inflammation<sup>1–4</sup>. The diversity of  $T_H1$  and  $T_H2$  function is not predetermined but depends on signals that drive the cells towards either subset<sup>1–4</sup>. Histamine, released from effector cells (mast cells and basophils) during inflammatory reactions can influence immune response<sup>5–8</sup>. Here we report that histamine enhances  $T_H1$ -type responses by triggering the histamine receptor type 1 (H1R), whereas both  $T_H1$ - and  $T_H2$ -type responses are negatively regulated by H2R through the activation of different biochemical intracellular signals. In mice, deletion of H1R results in suppression of interferon (IFN)- $\gamma$  and dominant secretion of  $T_H2$  cytokines (interleukin (IL)-4 and IL-13). Mutant mice lacking H2R showed upregulation of both  $T_H1$  and  $T_H2$  cytokines. Relevant to T-cell cytokine profiles, mice lacking H1R displayed increased specific antibody response with increased immunoglobulin- $\epsilon$  (IgE) and IgG1, IgG2b and IgG3 compared with mice lacking H2R. These findings account for an important regulatory mechanism in the control of inflammatory functions through effector-cell-derived histamine.