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Population ecology

# Local-scale impacts of extreme events drive demographic asynchrony in neighbouring top predator populations

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Extreme weather events are among the most critical aspects of climate change, but our understanding of their impacts on biological populations remains limited. Here, we exploit the rare opportunity provided by the availability of concurrent longitudinal demographic data on two neighbouring marine top predator populations (the black-browed albatross, *Thalassarche melanophris*, breeding in two nearby colonies) hit by an exceptionally violent storm during one study year. The aim of this study is to quantify the demographic impacts of extreme events on albatrosses and test the hypothesis that extreme events would synchronously decrease survival rates of neighbouring populations. Using demographic modelling we found that, contrary to our expectation, the storm affected the survival of albatrosses from only one of the two colonies, more than doubling the annual mortality rate compared to the study average. Furthermore, the effects of storms on adult survival would lead to substantial population declines (up to 2% per year) under simulated scenarios of increased storm frequencies. We, therefore, conclude that extreme events can result in very different local-scale impacts on sympatric populations. Crucially, by driving demographic asynchrony, extreme events can hamper our understanding of the demographic responses of wild populations to mean, long-term shifts in climate.

## 1. Introduction

As the Earth's climate continues to warm, many oceanic and atmospheric-physical processes are changing and will continue to do so in the coming century [1,2], with strong repercussions on ecosystems and biological populations [3–5]. Understanding the impacts of climate change on species and ecosystems has become a primary objective in ecological research and conservation science [6–8]. However, our capability to anticipate the effects of climate change on biological systems remains limited [9,10]. One of the major challenges is posed by the stochastic events associated with climate variability, which may amplify the responses of biological populations to the underlying changes in average climatic conditions [11,12].

Climate change is predicted to lead to increased climate variability, and increased frequency and intensity of extreme weather events [13]. Extreme events such as droughts, excessive precipitation, heat waves, hurricanes, tropical cyclones and storms [14–17] are among the most dramatic challenges faced by

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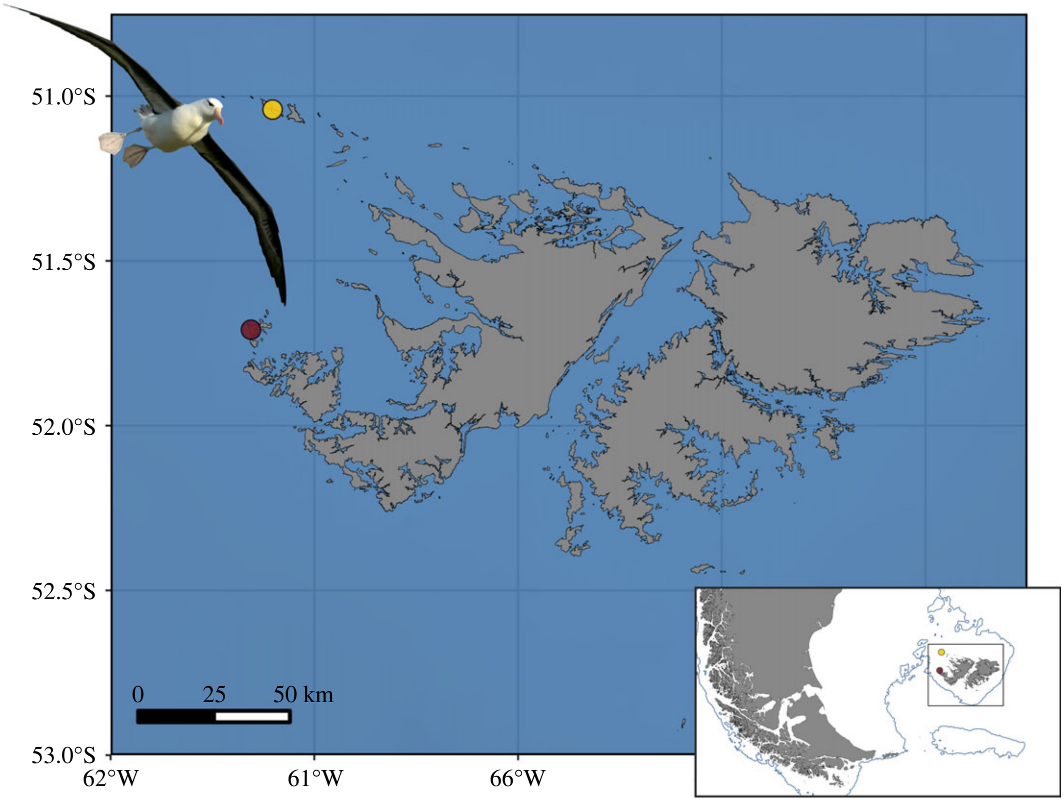

**Figure 1.** Map of the study area. The light and dark circles represent the study colonies of Steeple Jason and New Island, respectively. The inset map shows the location of our study colonies in the South Atlantic, with the 200 m isobath (blue line) representing the Patagonian Shelf.

already vulnerable biological and socio-economic systems [12,18–20]. Investigating the impacts of such events is particularly difficult because they are, by definition, rare [1]. Therefore, our understanding of the consequences of extreme events is limited compared to our knowledge of the species and ecosystem responses to long-term changes in climate [21]. In this context, long-term studies monitoring the population processes before, during and after extreme perturbations are among the most powerful tools to elucidate the demographic effects of extreme events on wild populations [22,23].

Here, we focus on two black-browed albatross (*Thalassarche melanophris*) populations breeding on nearby islands in the Falklands archipelago, South Atlantic Ocean (figure 1). The New Island and Steeple Jason colonies are just 75 km apart, with greatly overlapping foraging areas [24]. The distance between colonies is much smaller than that travelled by albatrosses during breeding, who often undertake foraging trips of over 1000 km [25]. Both colonies are the focus of an ongoing monitoring effort spanning nearly two decades. The study comprises the breeding season of 2010, when an exceptionally violent South Atlantic storm (wind speed estimated at 130–148 km $h^{-1}$ and open ocean swells of over 10 m) hit the Falklands' albatross colonies [26]. Field assessments of the storm impacts on Steeple Jason revealed that the more exposed areas experienced near-total breeding failure. Furthermore, over a hundred adult breeders were found dead on land, but many exhausted birds attempting to leave the colony may have been killed or severely injured by the large waves [26]. Despite this anecdotal evidence, it is unknown whether this discrete (i.e. a 'pulse' [27]) extreme perturbation affected albatross survival rate. The study system therefore offers a rare analytical viewpoint, enabling demographic comparisons of two nearby marine top-predator populations, monitored over the same timescale encompassing the occurrence of an extreme event.

Seabirds are marine top predators playing a critical role in structuring marine communities [28,29], regarded as sentinels and bioindicators of the health of the world oceans [29,30]. Investigating the co-occurrence of consistent demographic responses exhibited by multiple seabird populations (i.e. demographic 'synchronicity') may reveal critical insight into the effects of climate change on marine communities [31]. In long-lived species with delayed maturity such as seabirds [32], adult survival is the trait with highest elasticity, i.e. the main contributor to population growth rate. For these species, the theory of the canalization of life-history traits predicts that adult survival should exhibit limited fluctuations and be buffered (canalized) against environmental variability [33,34]. Besides its relevance for the conservation of these species, survival rate is therefore also the ideal candidate for a comparative study on the demographic effects of extreme events. In fact, if extreme perturbations are strong enough to impact the trait most strongly preserved against environmental variability (the adult survival rate) in one population, it is reasonable to expect concurrent effects also on the patterns of survival of nearby populations [31].

Here, we estimate the adult survival rates of black-browed albatrosses and address two overarching questions. First, we ask: *what are the potential future impacts on demography of the forecasted increase in frequency of extreme events*? Second, we ask: *within the same ecological context, do extreme events lead to concurrent increases in mortality, driving demographic synchrony in the survival rate of neighbouring populations*? This fine-scale demographic comparative approach is, to date, poorly represented in the ecological literature, and our research question remains largely unanswered.

## 2. Material and methods

Every year since 2003 (on New Island [35,36]) and 2006 (Steeple Jason), the monitoring effort produced a capture–mark–recapture dataset (ringing data of nesting adults and chicks) comprising an average of 250 (New Island) and 300 (Steeple Jason) yearly active nests (electronic supplementary material).

For each colony, we estimated the yearly apparent adult survival '$\phi$a' and resighting probability 'p' by analysing the ringing data of adult birds using a Bayesian Cormack–Jolly–Seber (CJS) model [37–39], only considering the encounter histories of nesting adults. To account for temporal variability in survival and resighting probabilities, we modelled them as the realization of a random process captured by a normal distribution with temporal variance $\sigma^2$ and mean $\mu$ (electronic supplementary material). The goodness of fit (GOF) of the model was evaluated using GOF Tests 2 and 3 (testing for homogeneity among cohorts and dependence within encounter histories, respectively) with the program RELEASE [40].

To evaluate the sensitivity of albatross to potential increases in frequency of extreme events, we carried out a prospective sensitivity analysis. We adopted a simulation framework based on the fine-scale output of the integrated population model (IPM) previously developed by Ventura *et al.* [36]. Starting from a theoretical population with same age–stage structure and same demographic rates as that on New Island in 2019 (i.e. the last season covered by the IPM [36]), we projected the population trajectory into the future. To do so, we drew all the demographic rates from the respective parameter posterior distributions estimated by the IPM [36], with the exception of adult survival $\phi$a, for which we considered four different scenarios, as follows.

Scenario 1. The same $\phi$a posterior distribution as that estimated by the New Island IPM, $\mu_{\phi a} = 0.941$, s.d. = 0.025.

Scenario 2. Same $\phi$a posterior distribution as above, but assuming that the population experienced the same $\phi$a quantified for Steeple Jason during the extreme weather event ($\mu_{\phi a} = 0.841$, s.d. = 0.013, see results) with mean probability = 0.05. This was equivalent to simulating the occurrence of one extreme event (and its consequent repercussions on the adult survival) every 20 years.

Scenario 3. Same as above, but assuming a probability of occurrence of an extreme event = 0.1, i.e. once every 10 years.

Scenario 4. Same as above, but assuming the probability of occurrence of an extreme event was set to 0.2, i.e. once every 5 years.

For each scenario, we projected the population dynamics for 100 years, repeating the simulation 100 times per scenario and measuring the overall breeding population growth $\lambda$ (electronic supplementary material).

## 3. Results

Overall, the apparent adult survival $\phi$a on Steeple Jason (mean = 0.924, s.d. = 0.023) was lower than that on New Island (mean = 0.933, s.d. = 0.021). However, when we excluded the 2011 survival estimate (i.e. measured between the 2010 and 2011 seasons, and therefore impacted by the extreme event), the overall $\phi$a on Steeple Jason (mean = 0.930, s.d. = 0.023) was closer to the survival estimated on New Island (mean = 0.932, s.d. = 0.021). In fact, the 2011 $\phi$a estimate on Steeple Jason was the lowest recorded in the study, estimated at mean = 0.841 (s.d. = 0.013) (figure 2*a*). Results of RELEASE GOF Test 3 indicated independence within encounter history and unbiased survival estimates. Test 2, however, suggested that different release cohorts required a different number of years to return to the colony after recruitment. While this may produce a bias in the detection rates, as undetected individuals are subsequently recaptured throughout the course of the long-term study the survival estimates are most likely unbiased and robust to the lack of fit in Test 2 (electronic supplementary material).

When considering the entire $\phi$a time series, the Steeple Jason and New Island posterior $\phi$a estimates had, on average, a weak positive correlation (Pearson's $r_{13} = 0.13$), with the 95% credible interval (CI) overlapping with 0 (CI: −0.15; 0.41). When we excluded 2011, the average correlation was stronger (Pearson's $r_{12} = 0.41$) and the CI did not overlap with 0 (CI: 0.04; 0.71).

The prospective sensitivity analysis shows that, based on the same structure and parametrization as in the New Island IPM [36] (scenario 1), the simulated albatross population has a projected slightly increasing trend, with an overall $\lambda$ estimated at 1.001 (s.d. = 0.003) (figure 2*b*). Under the same parametrization, but with the occurrence of an extreme weather event impacting adult survival every 20, 10 and 5 years (scenarios 2, 3 and 4, respectively) the population exhibits a decreasing trend, with overall $\lambda$ estimated at 0.996 (s.d. = 0.003), 0.991 (s.d. = 0.005) and 0.981 (s.d. = 0.006), respectively (figure 2*b*).

## 4. Discussion

Our demographic work shows the devastating impacts of an exceptionally violent storm on the survival of a longevous marine top predator. As the storm hit the Falklands in 2010, the adult survival rate dropped to a mean of 0.841 on Steeple Jason, the lowest rate ever estimated throughout the study. This value represents an increase in the annual mortality rate by a factor of 2.53 and of 2.10 compared to the previous season and to the colony mean survival, respectively. On New Island, however, the storm did not have the same impact on albatross survival, which was estimated at 0.949, i.e. the yearly mortality rate was less than half (0.32) of that estimated at Steeple Jason in the same year. These findings are in line with observational records suggesting that the storm killed hundreds of adult birds on the study colony on Steeple Jason [26], more exposed to the strong winds and wave action than that on New Island. Our findings are also in line with the growing evidence that extreme events do not only affect the reproductive success of seabirds [41–43]. Extreme weather events such as storms and hurricanes can also directly drive sharp reductions in the most conserved trait in long-lived birds, i.e. the survival of adult individuals [31,44,45]. For albatrosses and other longevous species, this conclusion has strong conservation implications [14].

In this context, our prospective population sensitivity analysis under higher storm frequencies scenarios—a trend documented in the South Atlantic Ocean [46]—suggests that the occurrence of a single storm of similar magnitude (i.e. with similar repercussions on survival) every two decades would be sufficient to drive a decreasing population trend (average yearly decrease of 0.41% in the long-term). With similar storms occurring once every 10 and 5 years, the population decline would be steeper (yearly decrease of 0.93% and 1.95%, respectively).

By contrast to our expectations, we found that, within the same geographical and ecological settings, extreme events

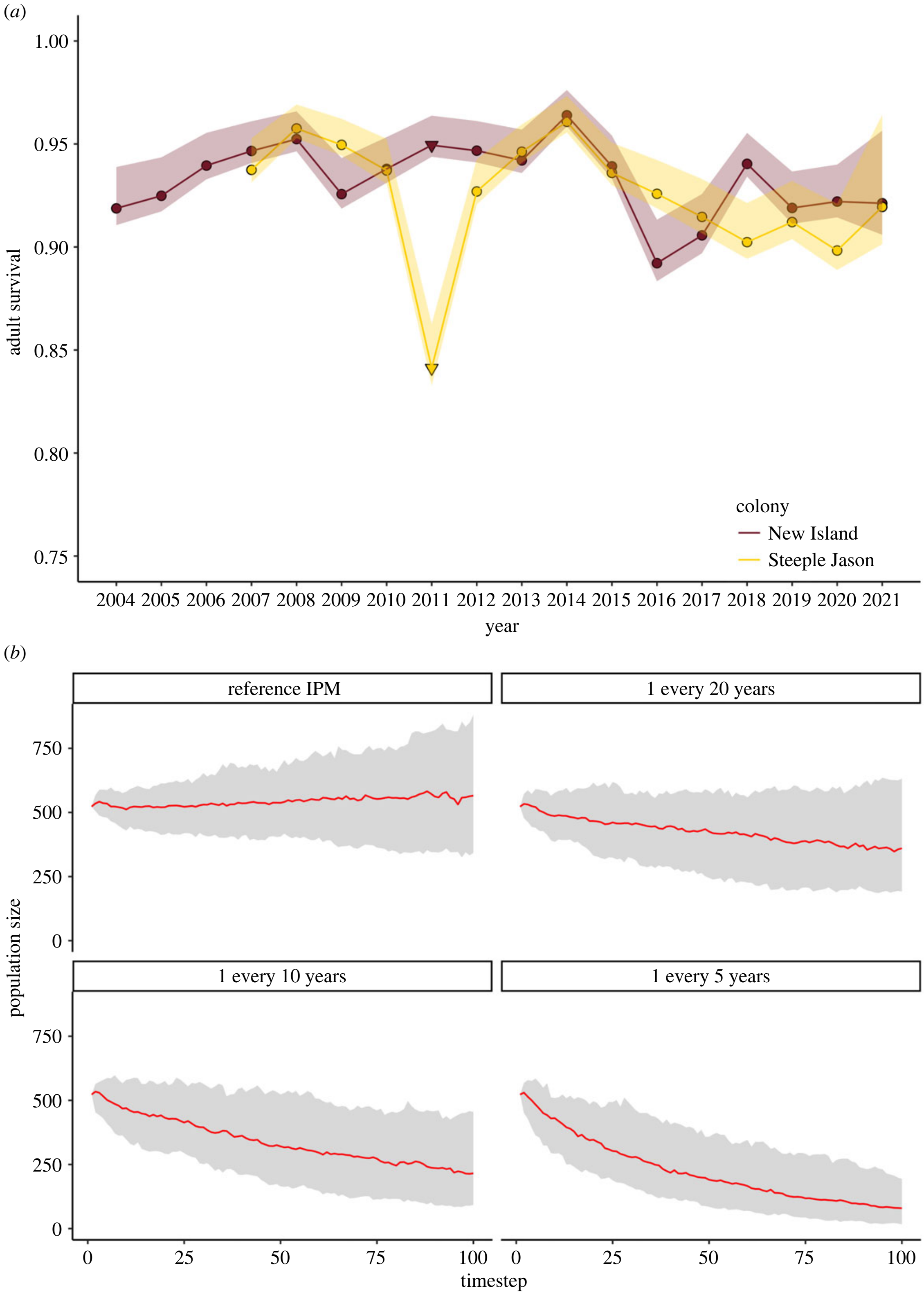

**Figure 2.** (*a*) The interannual variability in the survival of adult birds from the colonies of New Island (in dark) and Steeple Jason (light colour). (*b*) The impacts of increased extreme event frequency on the population dynamics of a simulated albatross population.

can have remarkably different demographic consequences in largely sympatric populations. As they elevate mortality in some populations but not in others, such events can drive demographic asynchrony even in highly conserved demographic traits of nearby populations. In this case study, the storm increased mortality on Steeple Jason but not on New Island. The resulting survival rates of the populations exhibited a significant correlation only after discarding the storm year from the analysis.

Extreme events are particularly difficult to understand, model and predict, representing in fact one of the World Climate Research Programme (WCRP) Grand Challenges [47]. Our work highlights that large-scale extreme events can interact with local-scale habitat characteristics (such as coast morphology and exposure to prevailing winds and swell direction), determining different demographic consequences on sympatric populations, driving demographic asynchrony and, ultimately, hindering our understanding of underlying ecosystem processes affecting wild populations [18]. This is particularly relevant, given the predicted increases in climate variability and in the frequency and intensity of extreme events brought by anthropogenic climate change [2]. From a management perspective, our study highlights that longitudinal studies on sentinel species (ideally, focussing on multiple sympatric populations) are among the most powerful diagnostic tools to elucidate the effects of rare, local extreme perturbations and, in turn, improve our understanding of the demographic responses of biological populations to mean, long-term shifts in climate.

**Ethics.** The monitoring programme and data collection were approved by the Falkland Islands Government, which granted the research licences R14/2007, R13/2011, R11/2013, R08/2014, R29/2017, R16/2020.

**Data accessibility.** The data, metadata and R scripts to reproduce the analysis are available at the Figshare digital repository: https://doi.org/10.6084/m9.figshare.20979064.v1 [48].

The data are provided in the electronic supplementary material [49].

**Authors' contributions.** F.V.: conceptualization, data curation, formal analysis, investigation, methodology, resources, software, validation, visualization, writing—original draft, writing—review and editing; A.S.: conceptualization, data curation, investigation, methodology, project administration, resources, software, writing—original draft, writing—review and editing; S.C.: data curation, investigation, methodology, resources, writing—original draft, writing—review and editing; A.K.: data curation, investigation, methodology, resources, writing—original draft, writing—review and editing; P.C.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We declare we have no competing interests.

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