Plastic behaviour buffers climate variability in the wandering albatross

Natasha Gillies[1*], Jack Thorley[1,2], Henri Weimerskirch[3], Stéphanie Jenouvrier[4], Christophe Barbraud[3], Karine Delord[3], Samantha C. Patrick[1]

[1]School of Environmental Sciences, University of Liverpool, Liverpool, UK
[2]Department of Zoology, University of Cambridge, Cambridge, UK
[3]Centre d'Études Biologiques de Chizé, UMR 7273 du CNRS-La Rochelle Université, 79360 Villiers-en-Bois, France
[4]Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA

*gilliesne@gmail.com

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ABSTRACT

Climate change has marked effects on global weather patterns and oceanic systems, impacting animal behaviour and fitness in potentially profound ways. Despite this, we lack detailed information about species' responses to climatic variation. Using an 11-year tracking dataset of over 300 individual birds, we explore the consequences of variation in the Southern Annular Mode (SAM) and Southern Oscillation Index (SOI) for individual behaviour and fitness in wandering albatrosses *Diomedea exulans* breeding in the Southern Indian Ocean. Our results reveal distinct responses between males and females to climatic variation that align with the impacts of each climatic index on the distinct foraging ranges of each sex. In positive SAM phases, linked to poorer foraging conditions in female ranges and better conditions in male ranges, females exhibited behaviour consistent with reduced foraging success: that is, fewer prey capture attempts, and more movement between feeding patches. Males, on the other hand, showed no behavioural change. During positive SOI phases, associated with good foraging conditions in both male and female foraging ranges, both sexes showed evidence of more successful foraging, with birds engaging in more search behaviour, and taking shorter trips with fewer prey capture attempts, together indicating increased food intake per unit time. We found limited evidence for a role of individual variation, as measured through differences in personality, suggesting that plastic responses to climate are sufficiently important so as to obscure inter-individual variation. Supporting this was the finding that individual breeding success was unaffected by climatic variation, suggesting that plastic foraging behaviour allows albatrosses to mitigate climate impacts and maintain reproductive output.

INTRODUCTION

Human impacts present a major threat to global biodiversity, with 20% of vertebrates now considered at risk of extinction, and climate change is recognised as playing a key role (Pereira et al. 2010; Bellard et al. 2012). Climate exerts profound influences on global weather patterns and oceanic systems, with significant downstream consequences for ecosystems and ecological dynamics. Understanding the ways in which animals respond to this is pertinent, particularly as significant increases in the intensity and frequency of extreme climate events are predicted for the coming decades (Easterling et al. 2000; Bailey and van de Pol 2016; Van De Pol et al. 2017; Wang et al. 2022). Yet while mounting evidence is demonstrating effects of climate on phenology, demography, and behaviour across a wide range of species (Selwood et al. 2015; Buchholz et al. 2019; Inouye 2022; Lewin et al. 2024), neither the mechanisms underpinning these effects, nor the relationships between them, are fully resolved.

In the face of environmental change, animals have three options, often summarised as ‘adapt, move, or die’: that is, they can adapt genetically, adjust their distribution or behaviour, or face extinction (Wong and Candolin 2015). For many long-lived vertebrate species, contemporary climate change may outpace genetic adaptation, leaving behavioural adjustment, such as through migratory range shifts (Lewin et al. 2024), changes in foraging effort (Speakman et al. 2021), or alterations to communication (Lengagne 2008), as the primary adaptive option. Behaviour therefore emerges as a crucial factor promoting species’ ability to cope with long-term environmental change. Behavioural plasticity, the ability of animals to adjust to environmental stimuli, varies considerably amongst individuals (Wilson 1998; Dall et al. 2004; Nussey et al. 2007; Stamps 2016), with potential impacts on the long-term persistence or trajectory of populations if subsets of populations cannot respond appropriately to changes in their environment. Understanding individual responses is therefore vital to predict species-level responses to climate change. Personality traits – particularly ‘boldness’, which typically measures the responses of individuals to novel stimuli (Sih et al. 2004; Patrick et al. 2013; Stamps and Biro 2016) – are increasingly recognised for their association with individual variation in behavioural plasticity (Dingemanse et al. 2010; Mathot and Dingemanse 2012; Stamps and Biro 2016; Gibelli and Dubois

2017). Shyer individuals are observed to be more responsive to environmental changes, while bolder individuals seem to be more fixed in their behaviours (Verbeek et al. 1994; Groothuis and Carere 2005; Coppens et al. 2010; Adriaenssens and Johnsson 2011; Gibelli and Dubois 2017). Personality may therefore offer a valuable, yet understudied, metric to assess individual variation in the capacity of animals to adapt to a changing climate.

In the marine environment, climate has been found to play important roles in behaviour, survival, and fitness in a number of species including southern elephant seals *Mirounga leonina* (Volzke et al. 2021), emperor penguins *Aptenodytes forsteri* (Jenouvrier et al. 2012), and blue petrels *Halobaena caerulea* (Guinet et al. 1998). Amongst marine fauna, seabirds offer particularly valuable indicators of the state of marine environments due to the ease of measuring their behaviour and demography, responsiveness to prey availability, sensitivity to weather conditions, and adaptable behaviour (Frederiksen et al. 2007; Parsons et al. 2008; Durant et al. 2009; Mallory et al. 2010). Species that cover large foraging distances are of particular interest due to their exposure to large temporal and spatial environmental variation.

Seabirds demonstrate flexible adjustment to rapid environmental change, but there are likely to be limits to this, as shown at a population level by the limited advancement of breeding phenology across seabirds (Keogan et al. 2018), despite consistent directional selection favouring earlier breeding in many cases (Reed et al. 2009; Dobson et al. 2017; Descamps et al. 2019). Additionally, the presence of repeatable individual behaviour, possibly reflecting fixed behavioural strategies, may constrain responses to environmental change (Patrick and Weimerskirch 2014; Ceia and Ramos 2015; Krüger et al. 2019). Climate-induced environmental changes can directly alter the energetic costs of behaviour, induce physiological stress, or lead to breeding failures or mass seabird wrecks during extreme weather events (Hass et al. 2012; Barbraud et al. 2015; Newell et al. 2015). Indirectly, changes in resource availability can have significant impacts. Seabirds are central-place foragers while breeding, meaning they face spatial constraints in access to resources, which can lead to spatio-temporal matchmismatch between their movement and resource availability (Grémillet and Boulinier 2009). This can lead to reduced survival and breeding success when individuals struggle to maintain foraging effort or success (e.g. Cory's shearwater *Calonectris borealis,* Pereira et al. 2020*;* northern gannet *Morus bassanus,* Montevecchi et al. 2021*;* king penguins *Aptenodytes patagonicus,* Le Bohec et al. 2008). Simultaneously investigating the impacts of climate on behaviour and fitness is therefore essential to predict how seabirds will fare in the face of ongoing climate change (Jenouvrier 2013; Jenouvrier et al. 2018).

Wandering albatrosses *Diomedea exulans* exhibit some of the longest - in both distance and duration - foraging trips amongst seabirds (Weimerskirch et al. 2014), during which they show high levels of responsiveness to environmental variation (Weimerskirch et al. 2000; Richardson et al. 2018) that varies amongst individuals (Gillies et al. 2023). Foraging behaviour differs markedly between the sexes, with males typically undertaking much longer trips to more southerly locations, and being much more dependent on high wind speeds for efficient movement (Shaffer et al. 2001; Wakefield et al. 2009; Clay et al. 2020). Age also plays a role, with older males undertaking longer-distance, more southerly foraging trips (Lecomte et al. 2010). Evidence that climate change may alter albatross behaviour is already emerging: increases in wind speeds in the Southern Ocean have been linked to improved breeding success, possibly due to reduced energetic costs when commuting during foraging flight (Weimerskirch et al. 2012). However, beyond wind, little is known about the potential impacts of environmental change on individual behaviour and breeding success in wandering albatrosses.

Disentangling the effects of environmental variation on behaviour, and ultimately, fitness, is complex. While single metrics such as sea surface temperature (SST) or air temperature, have been linked to changes in behaviour and phenology (e.g. loggerhead turtles *Caretta caretta,* Mazaris et al. 2008; Western Australian Magpies *Cracticus tibicen dorsalis,* Edwards et al. 2015), such measures offer only partial perspectives and capture relatively small-scale variation – in time, space, or both (Stenseth et al. 2002; Le Bohec et al. 2008). Climate indices offer consolidated measures that capture much broader variation in the environment, integrating information over large spatial and temporal scales. While this may come at a cost to fully understanding causative pathways of effects, such broad understanding can inform predictions about future responses to climate change, help identify potential adaptive responses and vulnerabilities, and provide a foundation for more detailed mechanistic studies, improving our ability to predict the impacts of expected future change.

Across the Southern Ocean, the leading modes of climate variation are the Southern Annular Mode (SAM) and Southern Oscillation Index (SOI; Rogers and van Loon 1982; Thompson and Wallace 2000; Fogt and Marshall 2020). SAM describes variability in the strength and position of a belt of westerly winds encircling the Antarctic, which contracts towards and expands away from the south pole during positive and negative phases respectively (Lovenduski and Gruber 2005; Fogt and Marshall 2020), with pronounced consequences for the wider environment dependent on latitude. Positive SAM phases enhance wind strength and upwelling south of the Antarctic Polar Front (approximately 50-60° S), where male wandering albatrosses primarily forage, while north of this, where females forage, the effects are opposite (Lovenduski and Gruber 2005). The Southern Oscillation Index measures sea level pressure differences between Tahiti and Darwin, Australia (Wang et al. 2016; Wang et al. 2022). Positive SOI, which at an extreme may indicate La Niña events, is linked to positive zonal wind stress - indicating strong westerly winds, decreases in SST, and increased upwelling across the Southern Ocean (Newell et al. 1982; McPhaden et al. 2020; Wang et al. 2022). Very negative values indicate El Niño events, a warming phase associated with decreased upwelling and weakened winds. Patterns of SAM and SOI are expected to change in the coming decades: climate models predict more frequent and intense El Niño/La Niña events and shifts in the intensity and position of the westerly winds associated with the SAM (Easterling et al. 2000; Fogt and Marshall 2020; McPhaden et al. 2020; Wang et al. 2022). Changes to both indices will have significant effects on oceanographic, atmospheric, and meteorological conditions.

We aimed to investigate how individual wandering albatrosses respond to SAM and SOI conditions and whether this affects their reproductive output. Changes in the SAM and SOI in the Southern Ocean have profound impacts on ocean currents and weather patterns at large spatial scales, which we anticipated would have behavioural consequences. Using an 11-year tracking dataset from the Crozet Islands in the Southern Indian Ocean, we investigated how changes in the SOI and SAM related to breeding success and foraging behaviour. By incorporating personality, a fixed trait known to constrain plasticity, we explored consistent individual variation in responses to these indices. By comparing individual responsiveness and breeding success changes, we aimed to indirectly assess how climate affects foraging behaviour and subsequent reproduction, giving essential insight into the capacity of albatrosses to buffer environmental variation and future climate change.

METHODS

GPS tracking

We tracked the movements of 346 wandering albatrosses (175 males, 171 females) during the incubation period (January to April) of 2010 to 2021. Albatrosses were sampled from Possession Island (Crozet Islands archipelago, Southern Indian Ocean, 46°24′ S, 51°46′ E). Since 1965, each year all adults and chicks in the study population have been captured by hand and equipped with a metal leg-ring and a plastic leg-ring bearing a unique identification number (Weimerskirch 2018). Adults are sexed based on size and plumage dimorphism within breeding pairs (Weimerskirch et al. 2005).

Each albatross was fitted with a GPS logger (IgotU 120/600, Mobile Action Technology, weighing up to 32g, max 0.5% body mass; X-GPS and Centurion, Sextant Technology, NZ weighing 60–75g, max 1.21% body mass; see details in Weimerskirch et al. 2018; Weimerskirch et al. 2020), which was deployed dorsally using thin strips of marine Tesa tape (Weimerskirch et al. 2014) and retrieved after the bird had completed at least one complete foraging trip. There is presently no evidence for an effect of such loggers on survival probability or breeding success in wandering albatrosses (Barbraud and Weimerskirch 2012). GPS loggers recorded fixes at frequencies ranging from 1 to 15 minutes, and the resulting data were resampled to give fixes at 15-minute intervals.

Measuring boldness

Every year, the ‘boldness’ of all birds in the Possession Island colony is measured by observing how individuals react to the approach of a human observer (see (Patrick et al. 2013) for full details). The observer noted each bird’s behaviours as they approached from a 5-meter distance, stopping short of the reaching the bird itself. Behaviours were recorded using a 5-point ordinal scale ranging from 0 to 4, where 0 = no response; 1 = bird lifts head; 2 = bird rises onto tarsi; 3 = bird vocalises; 4 = bird stands up. Using this scale, higher scores indicate bolder birds. Using these measurements, we estimated boldness by extracting individual-level best linear unbiased predictors from an ordinal generalised linear mixed model (GLMM) that was fitted to boldness scores using the `R` package `MCMCglmm`

(Hadfield 2010). The model has been used in previous studies of this population (Patrick et al. 2013; Gillies et al. 2023) and full details on the methodology can be found therein. The model included the fixed effects of observation number and observer ID (typically one observer per year), a random intercept for individual ID, and a random effect for the additive genetic variance, represented as the matrix of pairwise relatedness among all individuals.

Climate variables

Data on SAM indices were accessed from the National Center for Atmospheric Research Climate Data portal (https://legacy.bas.ac.uk/met/gjma/sam.html) on 2022-01-20 (Marshall 2003). Monthly SAM indices were calculated as numerical values representing the differences in monthly zonal sea level pressure at 40°S and 60°S. The data are observation-based, collected from six monitoring stations at each latitude. Monthly SOI indices were downloaded from the National Weather Service – Climate Prediction Center on 2022-01-20 (National Weather Service - Climate Prediction Center 2022). SOI is calculated as the standardised difference between anomalies in sea level pressure between Tahiti and Darwin, Australia, normalised by the monthly standard deviation. Further details available in the Appendix. SAM and SOI were not significantly correlated over the study period (Appendix).

Statistical analysis

All data processing and statistical analyses were carried out in `R` version 4.3.0 (R Core Team, 2023). Effects are presented as mean and [95% confidence interval] or mean ± standard deviation, unless otherwise specified. We interrogated fitted models by conducting diagnostic checks, including visual examination of residuals for normality, patterns, or trends, and assessing overdispersion using dispersion ratio checks.

Effect of climate on behaviour

We aimed to determine how climate indices influenced albatross foraging behaviour and reproductive success. First, we fitted a three-state hidden Markov model (HMM) to the GPS tracking dataset using the R package `momentuHMM` (McClintock and Michelot 2018) in order to categorise 15-minute fixes

GPS into the three discrete behavioural states: rest, travel, and search. Models were fitted to males and females separate due to their known differences in movement behaviour (Shaffer et al. 2001; Clay et al. 2020; Gillies et al. 2023). Step length and turning angle were used as input variables, modelled with a Von Mises and a Gamma distribution respectively, and previous studies that made use of this dataset were used to guide parameterisation (Clay et al. 2020; Gillies et al. 2023). Using these inputs, the model identified rest as fixes with low speeds and low to moderately concentrated turning angles, search as fixes with moderate speeds and moderate to wide turning angles, and travel as fixes with high speeds and concentrated turning angles.

From these three broad behavioural categories, we calculated metrics of foraging behaviour that would be most likely to be shaped by climate: the number of landings per day of the foraging trip, the ratio of time spent in search relative to travel, the total distance covered over the trip in kilometres, and the median distance travelled between search bouts (justification in Appendix). We fitted GLMMs to each metric, with the fixed effects of monthly climate index (SAM or SOI), boldness, and their interaction using the `glmmTMB` package in R (Brooks et al. 2017). We controlled for age, which is also known to affect foraging behaviour in wandering albatrosses (Lecomte et al. 2010; Froy et al. 2015), by including it as a fixed effect. Models were fitted separately for each sex and climate index (SAM or SOI) to reduce model complexity and therefore aid convergence and interpretation. All models included individual ID and year as random effects to account for repeated measures of the same individuals over time and annual variation, respectively. Total distance and median distance between search bouts was modelled with a Gamma distribution with a log link to reflect the positive right skewed nature of the response. Ratio of search relative to travel was modelled with a beta distribution due to its proportional nature. As a discrete count variable, number of landings per day was modelled with a Poisson distribution.

Effect of climate on reproductive success

We next examined the relationship between climatic variation and breeding to determine whether effects of climate on reproduction might be indirectly mediated by effects on foraging behaviour. Existing literature suggests that either SAM and SOI could have impacts prior to, during the breeding season, or both. We therefore averaged the monthly values of each index for September and November (pre-breeding) and January to April (breeding). December was excluded as a mixture of pre-breeding and breeding activity takes place during this month.

We considered available breeding success data for the entire Possession Island population, gathered between 1980 and 2020 (3052 individuals), to maximise available variation in the SAM and SOI. We fitted binomial GLMMs to the binomial variable current 'breeding success' (success vs failure), which considered only those birds that attempted to breed. To reduce model complexity, each climate index was fitted in a separate model. Models included the fixed effects of mean breeding and pre-breeding climate index (SAM or SOI respectively), age, and boldness. Interactions between age and each climate index (breeding and pre-breeding) were included to account for the idea that older or younger individuals may be differentially equipped to cope with environmental variation; a further three-way interaction was included between age, climate index, and boldness to account for the additional effect that boldness may have on this relationship. Non-significant interaction terms were removed from the model to ensure accurate appraisal of fixed effects (Engqvist 2005). Age was incorporated as a quadratic predictor, due to its known curvilinear association with breeding success (Weimerskirch 1992). All variables were centred and scaled to aid model convergence and interpretation of effects. Models were fitted for each sex separately due to known sex-related differences in responses to the environment (Weimerskirch et al. 2018; Clay et al. 2020) and to avoid the involvement of complex four-way interactions. Individual ID and year were included as random effects to control for repeated individual measures and interannual variation respectively.

Ethics

All handling and experimental procedures were conducted in accordance with guidance and rules issued by the Réserve Nationale des Terres Australes. All field protocols and manipulations were granted approval by the Comité National de la Protection de la Nature and the ‘Préfet of Terres Australes et Antarctiques Françaises’ to Program IPEV N°109.

RESULTS

We obtained 690 foraging trips, giving an average of 2.02 ± 1.41 trips per bird. Trips lasted a mean 8.1 ± 5.7 days. As previously reported (Weimerskirch et al., 2012a), females had more northerly foraging distributions compared to males (Figure 1).

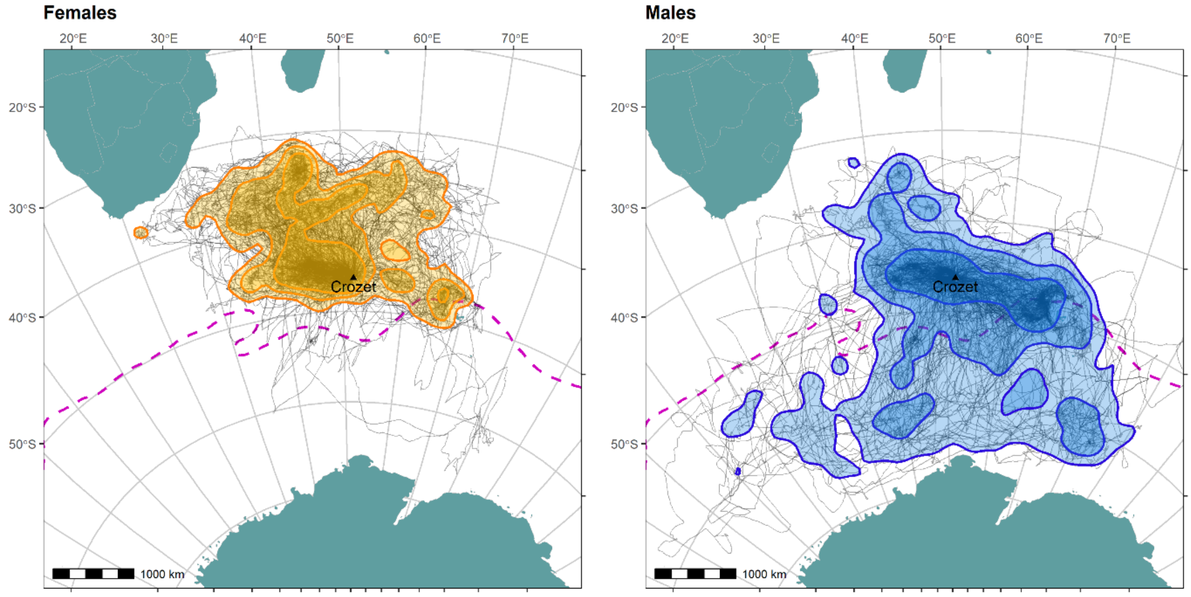

Figure 1. *Foraging tracks of wandering albatrosses Diomedea exulans tracked during the study. Possession Island indicated with black triangle. Grey tracks show individual bird movements; shaded polygons indicate 90% (lightest), 75% (mid), and 50% (darkest) utilisation distributions for all females (yellow polygons) and males (blue polygons). Pink dotted line shows approximate location of Antarctic Polar Front (Orsi and Harris 2019). Map and GPS tracks displayed in a Lambert azimuthal equal-area projection, centred on Possession Island.*

Over the past 60 years, SAM has shown a gradual tendency to become more positive over time (β = 0.02 ± 0.004, t = 5.11, p < 0.001), while SOI has been relatively stable (β = 0.002 ± 0.007, t = 0.22, p = 0.83; Figure 2). The range of SAM and SOI values observed during the study period (SAM: -2.1- 4.9; SOI: -3.6, 4.5) were broad but did not encompass the most extreme negative indices observed over the range of the past 60 years (SAM: -7.7, 4.9; SOI: -6, 4.8).

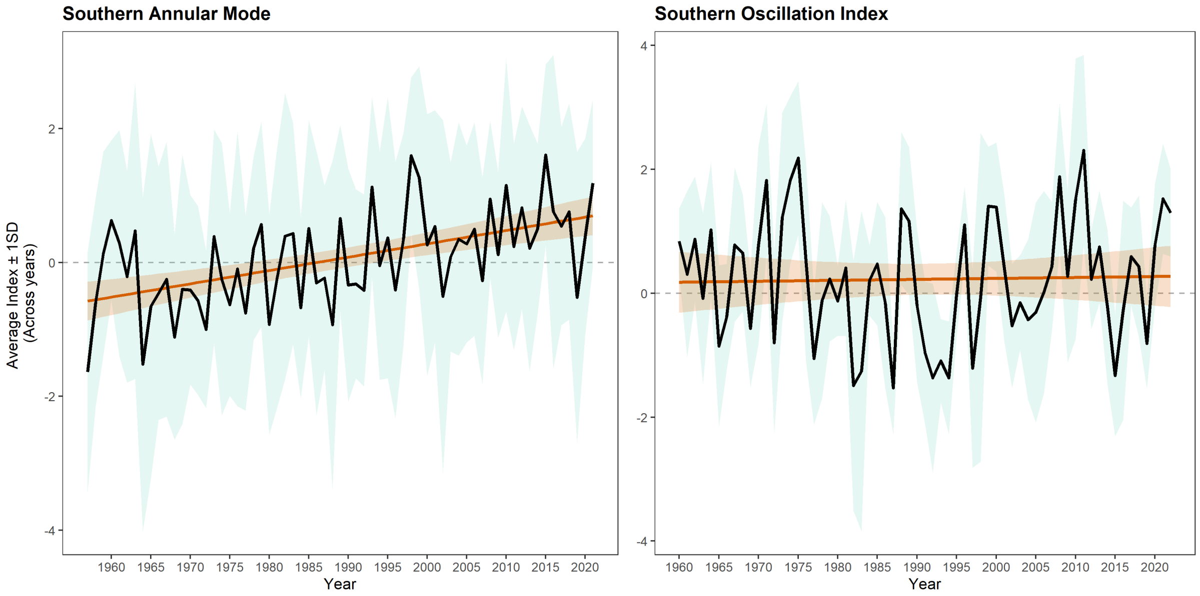

Figure 2. *Temporal trends in the Southern Annular Mode and Southern Oscillation Index. Black line shows changes in the annual average for each index; green-blue shading indicates standard error. Orange line and orange shading indicate regression and associated 95% confidence interval of change in index over time.*

Effect of climate on behaviour

While changes in the SOI were found to have significant effects on foraging behaviour for both males and females, only females were affected by changes in the SAM.

Females decreased the number of landings they made per day with increases in SAM and SOI (Figure 3, 4); males decreased their number of landings in response to SOI only (Figure 4, Table 1). For a one-point increase in SAM, females made 8.22 % fewer landings; for a one-point increase in SOI, they made 15.52 % fewer. Male responses to SOI depended on boldness. Shyer males had a reduced response to SOI, reducing landings by 10.24 % for a one-point increase in the SOI, while bolder birds reduced landings by 17.76 %. Overall, bolder males made more landings per day, with a mean of 23.7 landings per day versus 20.4 for shyer males.

The amount of time females spent in search behaviour relative to travel was affected by SAM conditions but not the SOI; males were unaffected by either index (Figure 3; Table 1). In positive SAM conditions, females reduced their search time relative to travel; a one-point increase in the SAM was associated with a 5.49 % decrease in time spent in search relative to travel.

We found that the total distance covered by birds on foraging trips decreased as SOI increased (Figure 3, Table 1). A one-point change in the SOI was associated with a 13.31 % decrease in travel distance for females and a 14.76 % change for males. There was no effect of SAM on total travel distance for either sex. However, for females, a one-point change in the SAM Was associated with a 5.03 % increase in the distance travelled between search bouts.

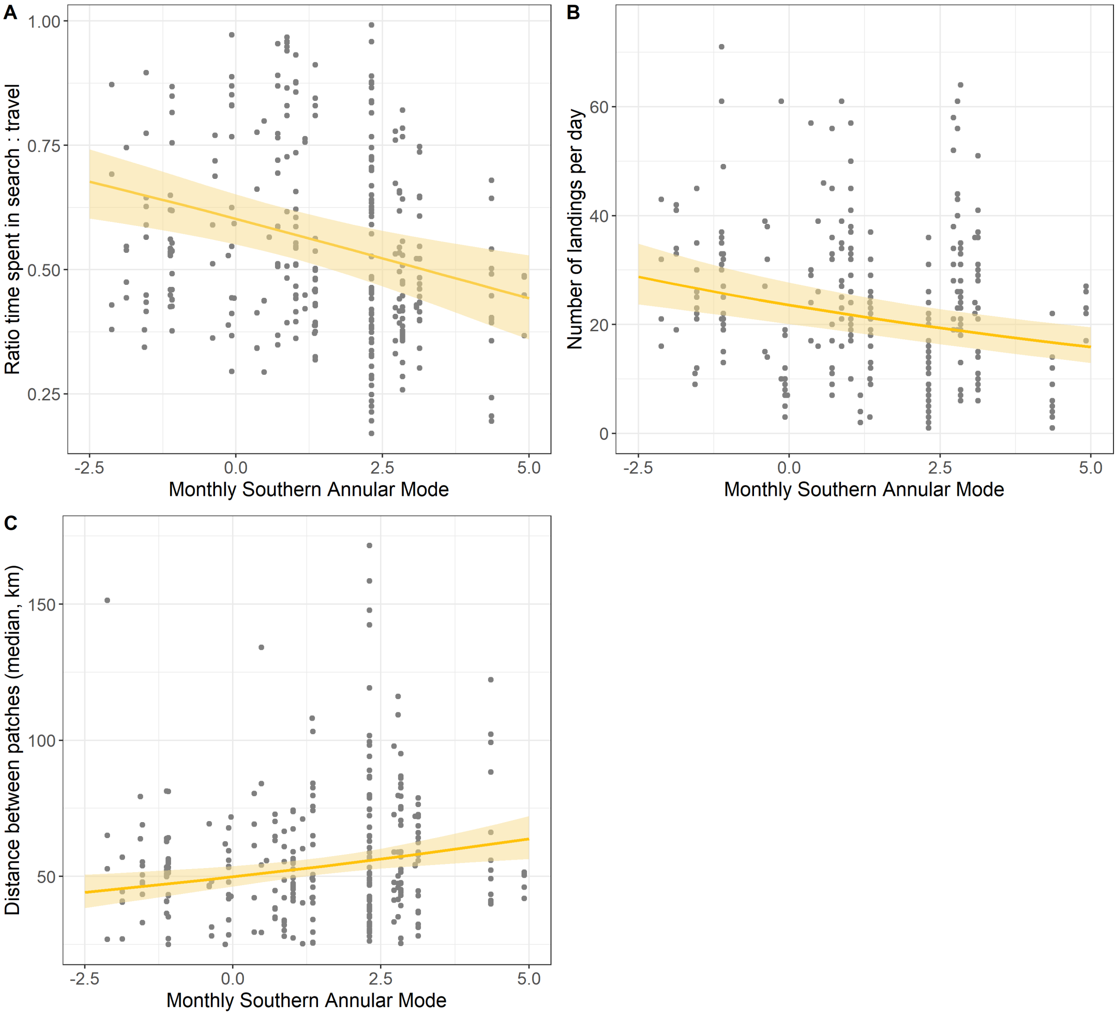

***Figure 3**. Effects of monthly Southern Annular Mode (SAM) on A, time spent in search relative to travel; B, number of landings per day of the foraging trip; and C, total distance travelled during foraging trips (km) for females. Lines and shaded areas indicate the regression and 95% confidence intervals for the effect of SAM. Each data point represents a single foraging trip.*

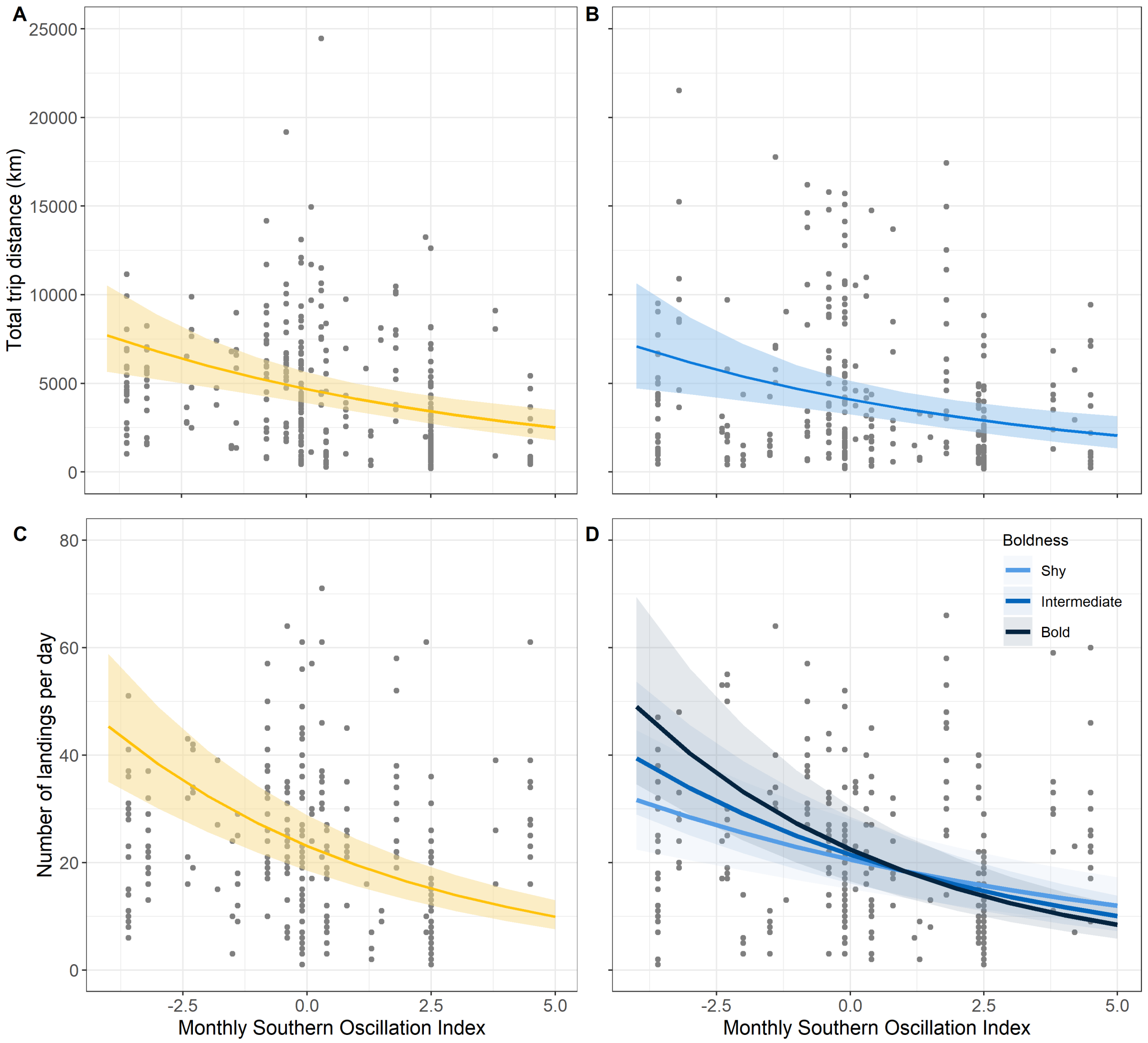

Figure 4. *Effects of monthly Southern Oscillation Index (SOI) on A, B, total distance travelled during foraging trips (km) and C, D, number of landings per day of the foraging trip for females in yellow and males in blue. Lines and shaded areas indicate the regression and 95% confidence intervals for the effect of SOI. Male responses in panel D are categorized by boldness, with lighter lines for shyer birds (10th percentile), intermediate lines for moderate birds (50th percentile), and darker lines for bolder birds (90th percentile). Each data point represents a single foraging trip.*

Table 1. *Model estimates from set of generalised linear mixed effects models examining the effect of the Southern Annular Mode (SAM) and Southern Oscillation Index (SOI) on foraging behaviour. Total path distance was fitted with a Gamma distribution (log link); ratio search: travel with a beta distribution, and landings per day with a Poisson distribution (log link): estimates are provided on the relevant link scale. An odds ratio of 1 suggests no effect, an odds ratio greater than 1 suggests a positive association, and an odds ratio less than 1 suggests a negative association. Significant p values and associated beta estimates and test statistics are highlighted in bold if they were found to be significant in both sexes; they are highlighted in bold and italics if they were found to be significant in only one sex. Non-significant interactions were dropped.*

Response	Predictor	Estimate (odds ratio*) and 95% confidence interval		z value		p value	
		F	***M***	***F***	***M***	***F***	***M***
Number of landings	***SAM***	***0.92 [0.89, 0.95]***	1.01 [0.98, 1.04]	***-4.80***	0.54	***< 0.001***	0.59
	Boldness	1.07 [0.99, 1.16]	1.01 [0.94, 1.09]	1.63	0.27	0.10	0.78
	Age	1.00 [0.99, 1.01]	1.01 [1.00, 1.02]	0.00	1.59	0.99	0.11
	SOI	**0.84 [0.82, 0.87]**	**0.85 [0.83, 0.88]**	**-10.41**	**-10.25**	**< 0.001**	**< 0.001**
	Boldness	1.07 [1.00, 1.15]	1.03 [0.96, 1.10]	1.84	0.71	0.066	0.48
	Age	1.00 [0.99, 1.01]	1.01 [1.00, 1.02]	-0.06	1.72	0.95	0.085
	SOI x boldness		***0.97 [0.96, 0.99]***		***-3.42***		***0.001***
Ratio search: travel	**SAM**	**0.8 [0.82, 0.94]**	**0.95 [0.90, 1.00]**	**-3.55**	**-1.94**	**< 0.001**	**0.003**
	Boldness	1.00 [0.92, 1.09]	0.95 [0.87, 1.03]	0.03	-1.23	0.98	0.053
	Age	1.00 [0.99, 1.01]	1.00 [0.99, 1.01]	-0.42	0.23	0.67	0.82
	SOI	1.03 [0.93, 1.13]	1.02 [0.97, 1.08]	0.57	0.78	0.57	0.43
	Boldness	0.99 [0.91, 1.08]	0.94 [0.87, 1.03]	-0.16	-1.37	0.87	0.17
	Age	1.00 [0.99, 1.01]	1.00 [0.99, 1.01]	-0.11	0.44	0.92	0.66
Total path distance (km)	SAM	1.04 [0.96, 1.12]	1.05 [0.97, 1.14]	1.00	1.26	0.32	0.21
	Boldness	1.04 [0.95, 1.15]	1.04 [0.94, 1.15]	0.92	0.74	0.36	0.46
	Age	1.00 [0.99, 1.01]	1.01 [1.00, 1.03]	-0.39	1.56	0.70	0.12
	SOI	**0.88 [0.83, 0.94]**	**0.87 [0.81, 0.94]**	**-4.16**	**-3.49**	**< 0.001**	**< 0.001**
	Boldness	1.05 [0.96, 1.15]	1.04 [0.94, 1.15]	1.14	0.82	0.25	0.41
	Age	1.00 [0.99, 1.01]	1.01 [1.00, 1.02]	-0.13	1.62	0.90	0.10
Median distance between search patches (km)	***SAM***	***1.05 [1.02, 1.08]***	1.03 [1.00, 1.07]	***3.06***	1.84	***0.002***	0.066
	Boldness	0.98 [0.94, 1.03]	1.02 [0.97, 1.07]	-0.69	0.91	0.49	0.36
	Age	1.00 [0.99, 1.00]	1.00 [1.00, 1.01]	-0.37	1.49	0.71	0.14
	SOI	1.00 [0.97, 1.02]	1.00 [0.97, 1.02]	-0.33	-0.20	0.74	0.85
	Boldness	0.99 [0.95, 1.04]	1.02 [0.98, 1.07]	-0.34	0.98	0.74	0.33
	Age	1.00 [0.99, 1.00]	1.00 [1.00, 1.01]	-0.86	1.34	0.39	0.18

*Estimate for number of landings is an Incidence Rate Ratio due to Poisson distribution.

Effect of climate on reproductive success

Mean breeding success for the entire Possession Island study colony between 1980 and 2020 was high at 77.96 ± 3.93% (mean weighted by annual sample size) and has been increasing annually (Table 2). We found no evidence for effects of SAM or SOI on individual breeding success for either sex, and no effect of boldness (Figure 5, Table 2). The relationship between age and breeding success was quadratic, with breeding success gradually increasing until around 25-30 years, at which point it declined.

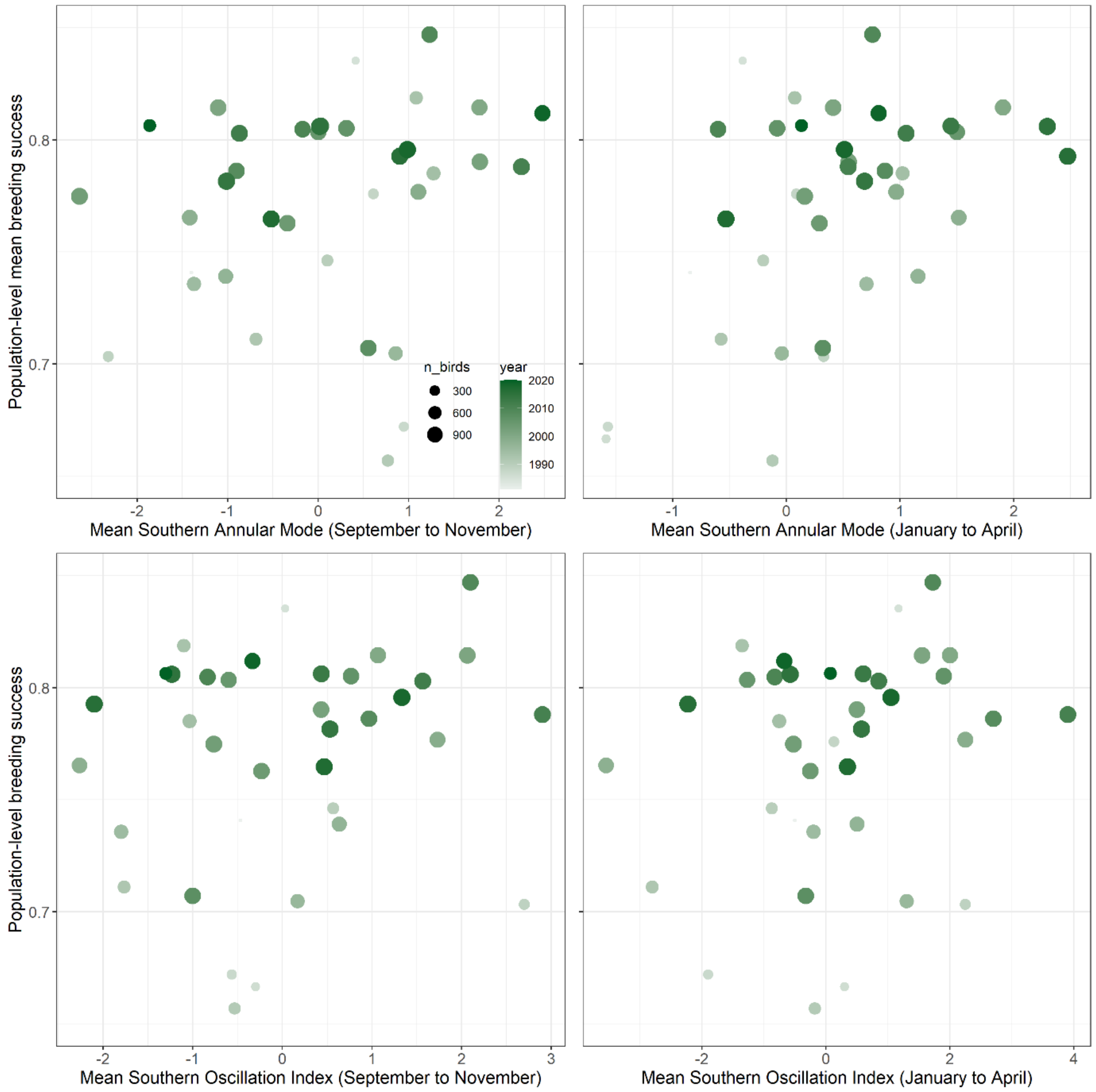

Figure 5. *Breeding success as a function of changes in the Southern Annular Mode and Southern Oscillation Index during breeding and pre-breeding periods. Points indicate mean breeding success for each year (labelled); size indicates sample for each year. Older year boxes coloured in lighter shades of green, more recent years in darker shades.*

Table 2. *Model estimates from binomial generalised linear mixed effects models examining the effect of the Southern Annular Mode (SAM) and Southern Oscillation Index (SOI), averaged (mean) for the breeding and non-breeding periods, on individual reproductive success. Non-significant interactive effects were iteratively dropped from the models. Significant p values and associated beta estimates and test statistics are highlighted in bold. Estimates are provided as odds ratios; an odds ratio of 1 suggests no effect, an odds ratio greater than 1 suggests a positive association, and an odds ratio less than 1 suggests a negative association.*

	Odds ratio and 95% confidence interval				**z value**				**p value**			
	SAM		**SOI**		**SAM**		**SOI**		**SAM**		**SOI**	
Predictor	***F***	***M***	***F***	***M***	***F***	***M***	***F***	***M***	***F***	***M***	***F***	***M***
Age	**1.23 (1.13, 1.33)**	**1.19 (1.10, 1.29)**	**1.23 (1.13, 1.33)**	**1.20 (1.11, 1.30)**	**4.90**	**4.33**	**4.94**	**4.50**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Age2	**0.82 (0.78, 0.87)**	**0.85 (0.81, 0.90)**	**0.82 (0.78, 0.87)**	**0.85 (0.81, 0.90)**	**-7.18**	**-5.98**	**-7.20**	**-6.00**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Mean SAM pre-breeding	0.98 (0.91, 1.05)	1.03 (0.94, 1.13)	1.06 (0.91, 1.23)	1.10 (0.92, 1.33)	-0.59	0.56	0.74	1.05	0.55	0.58	0.46	0.30
Mean SAM breeding	1.07 (0.99, 1.15)	1.06 (0.96, 1.18)	1.00 (0.86, 1.17)	1.00 (0.83, 1.20)	1.79	1.20	0.05	-0.03	0.073	0.23	0.96	0.98
Boldness	0.94 (0.87, 1.03)	0.97 (0.90, 1.05)	0.94 (0.86, 1.02)	0.97 (0.90, 1.05)	-1.36	-0.72	-1.40	-0.70	0.18	0.47	0.16	0.48

DISCUSSION

Over an 11-year period, we observed that climatic variation significantly impacted the behaviour of wandering albatrosses, yet did not impact their breeding success, suggesting that albatrosses are able to buffer the effects of climate on their foraging ecology to preserve their reproductive success. This work adds to a growing body of evidence suggesting that behavioural plasticity may be an essential mechanism by which animals can adjust to the changing environment and ultimately buffer the negative impacts of widescale climatic change (Bradshaw and Holzapfel 2006; Charmantier et al. 2008; Grémillet and Boulinier 2009; Moritz and Agudo 2013).

Variation in SAM differentially impacted the foraging ranges of female and male albatrosses. Positive SAM phases are associated with less favourable conditions for female foraging, marked by weaker winds and increased sea surface temperature (see Figure 1 in Lovenduski and Gruber 2005), and in such conditions females were found to land less frequently and to increase their travel time relative to searching. Landing is associated with prey capture attempts (Weimerskirch et al. 1997; Weimerskirch and Guionnet 2002), suggesting that females were making fewer attempts to capture prey items. Combined with observations that both relative travelling behaviour and the distance travelled between bouts of searching behaviour increased, this suggests that females were encountering fewer feeding patches during positive SAM phases. Conversely, positive SAM phase in male foraging ranges correlate with improved foraging conditions – specifically, increased wind speeds, cooler SST, and possibly increased chlorophyll levels. Despite this, male behaviour did not show adjustment in response to SAM. This may be due to the spatial variability of SAM effects, which tend to be beneficial in the south but disadvantageous in the north. As Figure 1 illustrates, males forage both north and south of the Antarctic Polar Front and so could experience improved or diminished foraging conditions depending on their chosen foraging location, potentially masking an overall relationship with foraging success. Alternatively, it is possible that this dichotomy emerges from between-sex differences in plasticity, a pattern that has been observed across a very small, but diverse, range of other species (Bonier et al. 2007; Meuthen et al. 2018; Brand et al. 2023). It is difficult, however, to disentangle this from the fact that females are also probably exposed to greater variation in foraging habitat quality as they typically forage north of the Antarctic Polar Front, where oceanographic conditions are more variable. Conditions in male foraging grounds are generally good for foraging, being characterised by stronger winds and cooler temperatures, and so further positive change may not have had detectable effects (Wakefield et al. 2009; Clay et al. 2020). The increasing trend for positive SAM in recent years may further obscure effects on male behaviour (Figure 3; Abram et al. 2014; Fogt and Marshall 2020).

Variation in SOI affects female and male foraging ranges similarly, with positive phases correlating with cooler SST and stronger winds, the former being thought to indicate better foraging conditions while the latter makes at-sea travel more efficient (Richardson et al. 2018; Evans et al. 2021). During positive SOI phases, both sexes showed behaviours that in combination may indicate successful foraging; that is, fewer landings and shorter foraging distances (thought to be indicative of successful trips; Salamolard and Weimerskirch 1993; Shaffer et al. 2003; Weimerskirch et al. 2007). Females additionally spent more time in search behaviour. These responses may suggest birds were experiencing more successful foraging trips, making fewer prey capture attempts that were either more successful or resulted in the capture of more or larger prey. While it is unclear why males responded to SOI variation, but not SAM, the greater variability in SOI during the study period may have made its effects more detectable as compared to SAM.

By incorporating the metric ‘boldness’ in our analyses, we aimed to quantify the role of individual variation in responses to climate. Overall, boldness had a limited impact on individual behavioural responses to longer-term environmental change: personality was only found to be important in male responses to the SOI, where shy males were found to adjust their number of landings to a lesser extent than bolder males, contrasting with theoretical work predicting that shyer individuals should be more attuned to their environment (Mathot and Dingemanse 2012; Snell-Rood 2013; Stamps 2016; Gibelli and Dubois 2017), though this effect was modest. Female responses did not depend on personality, a surprising result given that previous work indicates that boldness influences short-term behavioural responses to specific environmental factors, such as instantaneous wind conditions, in female wandering albatrosses (Gillies et al. 2023). This is unlikely to reflect a lack of perceived 'risk' as birds experienced a full spectrum of environmental conditions, which should include both 'risky' and 'non-risky' scenarios. Instead, this discrepancy indicates that while personality traits may affect immediate, short-term behavioural adjustments, they might not significantly impact long-term responses to broader climatic factors. This is consistent with previous findings that boldness has a minimal impact on female demographic rates (Van de Walle et al. 2024) and overall breeding success (Gillies et al. 2023). These findings support the idea that behavioural plasticity is a crucial mechanism by which species buffer potential impacts of environmental variation on their fitness (Komers 1997; Chevin et al. 2010; Beever et al. 2017).

As albatrosses are long-lived and thus prioritise self-maintenance over reproductive investment, poor foraging conditions during the breeding season could negatively impact their offspring's survival and development through reduced care or provisioning quality (Stearns 1992). Despite this, we found no effect of SAM or SOI on individual breeding success. It is possible that negative impacts on female foraging were offset by the success of their male partners, given the contrasting impacts on their respective foraging ranges. Alternatively, or additionally, albatrosses may have mechanisms to mitigate environmental impacts before they impact reproductive output. As capital breeders, the costs of reproduction in wandering albatrosses are likely to be paid from resources accumulated prior to breeding, with resources gained during the breeding season being allocated to maintaining parental condition rather than being passed to offspring (Jonsson 1997). Indeed, previous work has shown that albatrosses experiencing improved foraging conditions during provisioning do not invest this extra energy into their chick (Berrow and Croxall 2001). However, our measure of breeding success considers only chick survival until fledging, and so may not capture long-term fitness impacts. Previous research indicates potential cohort effects due to environmental variation (Fay et al. 2015; Fay et al. 2016), highlighting the need for additional measures such as chick body condition and recruitment to fully understand the fitness impacts of climatic variation on albatrosses. Furthermore, conditions during the pre-breeding season can have significant consequences for the probability of attempting to breed, even if it does not have effects on breeding success directly (Van de Walle et al. 2024). Future studies should explore potential long-term effects on reproduction, including impacts on offspring quality, breeding frequency and probability, or reproductive lifespan, given known carry-over effects from current to future reproduction in seabirds (Catry et al. 2013; Fayet et al. 2016; Moe et al. 2017; Harris et al. 2020).

Ultimately, the finding that breeding success was unaffected by climatic variation may suggest that all individuals are selected to behaviourally buffer this variation, at least within a season. This may additionally help explain the finding that personality did not have strong effects on behaviour, if responses to climate are so conserved that they mask any potential effects of boldness. However, our study captures only an 11-year snapshot of climatic variation, during which time the most extreme negative values of SAM and SOI were not observed. Wandering albatrosses are capable of considerable behavioural feats, travelling several thousand kilometres in a single foraging trip, and so are adept at behaviourally buffering variation, something that has also been observed in their responses to long-term changes in wind conditions (Weimerskirch et al. 2012). However, there are almost certainly limits to the environmental variation that birds can withstand. Indeed, previous work has found that wandering albatrosses do have a maximum tolerable wind speed that they act to avoid (Nourani et al. 2023), suggesting that more extreme variation could in theory lead to among-individual differences in responses that we were unable to capture. Furthermore, as the breeding season progresses, the ability to buffer environmental variation may become particularly critical as the chick hatches and the energetic demands of provisioning therefore increase. Such demands may restrict the capacity of albatrosses' behavioural coping mechanisms, which could significantly affect foraging efficiency and, consequently, reproductive success.

Our study sheds light on the relationship between climatic variation, foraging behaviour, and reproductive success in wandering albatrosses. While we observed significant impacts of changes in

SAM and SOI on foraging behaviour, these did not translate into effects on reproductive success. This suggests that the behavioural plasticity exhibited by seabirds, including albatrosses, may provide some protection against the broader effects of climate warming. However, it remains unclear whether environmental effects may still impact overall fitness, or whether small effects that are undetectable at this scale could accumulate over albatrosses' entire lifecycles. Moreover, this plasticity is unlikely to be limitless (Somveille et al. 2020), particularly as climate variability intensifies, exposing animals to extremes of environmental variation to which they cannot adapt. Seabirds have already experienced mass die-offs, wrecks, and heat stress associated with extremes of wind and temperature (Lempidakis et al. 2022; Nourani et al. 2023). Similar trends have been observed for terrestrial species when extreme conditions exceed the capacity of species to behaviourally adjust or lead to the expression of catastrophically maladaptive behaviour (Santini et al. 2016; van Baaren and Candolin 2018; Sharpe et al. 2021). Such effects may be compounded by anthropogenic impacts such as fishing, introduced predators, land-use change, or pollutants (Thuiller et al. 2006; Goutte et al. 2014; Oro 2014; Barbraud et al. 2021). Our results offer insight into these complex dynamics, highlighting the importance of understanding the limits of behavioural plasticity and how it interacts with anthropogenic pressures to predict the likely fate of species in our changing environment.

REFERENCES

Abram NJ, Mulvaney R, Vimeux F, Phipps SJ, Turner J, England MH. 2014. Evolution of the Southern Annular Mode during the past millennium. Nature Clim Change. 4(7):564–569. doi:10.1038/nclimate2235.

Adriaenssens B, Johnsson JI. 2011. Shy trout grow faster: exploring links between personality and fitness-related traits in the wild. Behavioral Ecology. 22(1):135–143. doi:10.1093/beheco/arq185.

van Baaren J, Candolin U. 2018. Plasticity in a changing world: behavioural responses to human perturbations. Current Opinion in Insect Science. 27:21–25. doi:10.1016/j.cois.2018.02.003.

Bailey LD, van de Pol M. 2016. Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. Journal of Animal Ecology. 85(1):85–96. doi:10.1111/1365-2656.12451.

Barbraud C, Delord K, Weimerskirch H. 2015. Extreme ecological response of a seabird community to unprecedented sea ice cover. R Soc open sci. 2(5):140456. doi:10.1098/rsos.140456.

Barbraud C, des Monstiers B, Chaigne A, Marteau C, Weimerskirch H, Delord K. 2021. Predation by feral cats threatens great albatrosses. Biol Invasions. 23(8):2389–2405. doi:10.1007/s10530-021-02512-9.

Barbraud C, Weimerskirch H. 2012. Assessing the effect of satellite transmitters on the demography of the Wandering Albatross Diomedea exulans. J Ornithol. 153(2):375–383. doi:10.1007/s10336-011-0752-8.

Beever EA, Hall LE, Varner J, Loosen AE, Dunham JB, Gahl MK, Smith FA, Lawler JJ. 2017. Behavioral flexibility as a mechanism for coping with climate change. Frontiers in Ecol & Environ. 15(6):299–308. doi:10.1002/fee.1502.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters. 15(4):365–377. doi:10.1111/j.1461-0248.2011.01736.x.

Berrow SD, Croxall JP. 2001. Provisioning Rate and Attendance Patterns of Wandering Albatrosses at Bird Island, South Georgia. The Condor. 103(2):230–239. doi:10.1093/condor/103.2.230.

Bonier F, Martin PR, Sheldon KS, Jensen JP, Foltz SL, Wingfield JC. 2007. Sex-specific consequences of life in the city. Behavioral Ecology. 18(1):121–129. doi:10.1093/beheco/arl050.

Bradshaw WE, Holzapfel CM. 2006. Evolutionary response to rapid climate change. Science. 312(5779):1477–1478. doi:10.1126/science.1127000.

Brand JA, Yee WKW, Aitkenhead IJ, Martin JM, Polverino G, Chown SL, Wong BBM, Dowling DK. 2023. Temperature change exerts sex-specific effects on behavioural variation. Proc R Soc B. 290(2002):20230110. doi:10.1098/rspb.2023.0110.

Brooks M E, Kristensen K, Benthem K J ,van, Magnusson A, Berg C W, Nielsen A, Skaug H J, Mächler M, Bolker B M. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal. 9(2):378. doi:10.32614/RJ-2017-066.

Buchholz R, Banusiewicz JD, Burgess S, Crocker-Buta S, Eveland L, Fuller L. 2019. Behavioural research priorities for the study of animal response to climate change. Animal Behaviour. 150:127–137. doi:10.1016/j.anbehav.2019.02.005.

Catry P, Dias MP, Phillips RA, Granadeiro JP. 2013. Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: An experimental demonstration. Ecology. 94(6):1230–1235. doi:10.1890/12-2177.1.

Ceia FR, Ramos JA. 2015. Individual specialization in the foraging and feeding strategies of seabirds: a review. Marine Biology. 162(10):1923–1938. doi:10.1007/s00227-015-2735-4.

Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LEB, Sheldon BC. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science. 320(5877):800–803. doi:10.1126/science.1157174.

Chevin L-M, Lande R, Mace GM. 2010. Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. Kingsolver JG, editor. PLoS Biol. 8(4):e1000357. doi:10.1371/journal.pbio.1000357.

Clay TA, Joo R, Weimerskirch H, Phillips RA, den Ouden O, Basille M, Clusella-Trullas S, Assink JD, Patrick SC. 2020. Sex-specific effects of wind on the flight decisions of a sexually dimorphic soaring bird. Journal of Animal Ecology. 89(8):1811–1823. doi:10.1111/1365-2656.13267.

Coppens CM, de Boer SF, Koolhaas JM. 2010. Coping styles and behavioural flexibility: towards underlying mechanisms. Philosophical Transactions of the Royal Society B: Biological Sciences. 365(1560):4021–4028. doi:10.1098/rstb.2010.0217.

Dall SRX, Houston AI, McNamara JM. 2004. The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. Ecology Letters. 7(8):734–739. doi:10.1111/j.1461-0248.2004.00618.x.

Descamps S, Ramírez F, Benjaminsen S, Anker-Nilssen T, Barrett RT, Burr Z, Christensen-Dalsgaard S, Erikstad K, Irons DB, Lorentsen S, et al. 2019. Diverging phenological responses of Arctic seabirds to an earlier spring. Global Change Biology. 25(12):4081–4091. doi:10.1111/gcb.14780.

Dingemanse NJ, Kazem AJN, Réale D, Wright J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends in Ecology and Evolution. 25(2):81–89. doi:10.1016/j.tree.2009.07.013.

Dobson FS, Becker PH, Arnaud CM, Bouwhuis S, Charmantier A. 2017. Plasticity results in delayed breeding in a long-distant migrant seabird. Ecology and Evolution. 7(9):3100–3109. doi:10.1002/ece3.2777.

Durant J, Hjermann D, Frederiksen M, Charrassin J, Le Maho Y, Sabarros P, Crawford R, Stenseth N. 2009. Pros and cons of using seabirds as ecological indicators. Clim Res. 39(2):115–129. doi:10.3354/cr00798.

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO. 2000. Climate extremes: Observations, modeling, and impacts. Science. 289(5487):2068–2074. doi:https://doi.org/10.1126/science.289.5487.2068.

Edwards EK, Mitchell NJ, Ridley AR. 2015. The impact of high temperatures on foraging behaviour and body condition in the Western Australian Magpie Cracticus tibicen dorsalis. Ostrich. 86(1–2):137–144. doi:10.2989/00306525.2015.1034219.

Engqvist L. 2005. The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. Animal Behaviour. 70(4):967–971. doi:10.1016/j.anbehav.2005.01.016.

Evans R, Lea M-A, Hindell MA. 2021. Predicting the distribution of foraging seabirds during a period of heightened environmental variability. Ecological Applications. 31(5):e02343. doi:10.1002/eap.2343.

Fay R, Barbraud C, Delord K, Weimerskirch H. 2016. Variation in the age of first reproduction: different strategies or individual quality? Ecology. 97(7):1842–1851. doi:10.1890/15-1485.1.

Fay R, Weimerskirch H, Delord K, Barbraud C. 2015. Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. Boulinier T, editor. Journal of Animal Ecology. 84(5):1423–1433. doi:10.1111/1365-2656.12390.

Fayet AL, Freeman R, Shoji A, Kirk HL, Padget O, Perrins CM, Guilford T. 2016. Carry-over effects on the annual cycle of a migratory seabird: an experimental study. Journal of Animal Ecology. 85(6):1516–1527. doi:10.1111/1365-2656.12580.

Fogt RL, Marshall GJ. 2020. The Southern Annular Mode: Variability, trends, and climate impacts across the Southern Hemisphere. Wiley Interdisciplinary Reviews: Climate Change. 11(4). doi:10.1002/wcc.652.

Frederiksen M, Mavor R, Wanless S. 2007. Seabirds as environmental indicators: the advantages of combining data sets. Mar Ecol Prog Ser. 352:205–211. doi:10.3354/meps07071.

Froy H, Lewis S, Catry P, Bishop CM, Forster IP, Fukuda A, Higuchi H, Phalan B, Xavier JC, Nussey DH, et al. 2015. Age-Related Variation in Foraging Behaviour in the Wandering Albatross at South Georgia: No Evidence for Senescence. Descamps S, editor. PLoS ONE. 10(1):e0116415. doi:10.1371/journal.pone.0116415.

Gibelli J, Dubois F. 2017. Does personality affect the ability of individuals to track and respond to changing conditions? Behavioral Ecology. 28(1):101–107. doi:10.1093/BEHECO/ARW137.

Gillies N, Weimerskirch H, Thorley J, Clay TA, Martín López LM, Joo R, Basille M, Patrick SC. 2023. Boldness predicts plasticity in flight responses to winds. Journal of Animal Ecology.(June):1–13. doi:10.1111/1365-2656.13968.

Goutte A, Barbraud C, Meillère A, Carravieri A, Bustamante P, Labadie P, Budzinski H, Delord K, Cherel Y, Weimerskirch H, et al. 2014. Demographic consequences of heavy metals and persistent organic pollutants in a vulnerable long-lived bird, the wandering albatross. Proc R Soc B. 281(1787):20133313. doi:10.1098/rspb.2013.3313.

Grémillet D, Boulinier T. 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. Mar Ecol Prog Ser. 391:121–137. doi:10.3354/meps08212.

Groothuis TGG, Carere C. 2005. Avian personalities: characterization and epigenesis. Neuroscience & Biobehavioral Reviews. 29(1):137–150. doi:10.1016/j.neubiorev.2004.06.010.

Guinet C, Chastel O, Koudil M, Durbec JP, Jouventin P. 1998. Effects of warm sea-surface temperature anomalies on the blue petrel at the Kerguelen Islands. Proceedings of the Royal Society B: Biological Sciences. 265(1400):1001–1006. doi:10.1098/rspb.1998.0390.

Hadfield JD. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. Journal of Statistical Software. 33(2):1–22.

Harris SM, Descamps S, Sneddon LU, Cairo M, Bertrand P, Patrick SC. 2020. Personality-specific carry-over effects on breeding: Personality-specific carry-over effects. Proceedings of the Royal Society B: Biological Sciences. 287(1940). doi:10.1098/rspb.2020.2381rspb20202381.

Hass T, Hyman J, Semmens B. 2012. Climate change, heightened hurricane activity, and extinction risk for an endangered tropical seabird, the black-capped petrel Pterodroma hasitata. Mar Ecol Prog Ser. 454:251–261. doi:10.3354/meps09723.

Inouye DW. 2022. Climate change and phenology. WIREs Climate Change. 13(3):e764. doi:10.1002/wcc.764.

Jenouvrier S. 2013. Impacts of climate change on avian populations. Global Change Biology. 19(7):2036–2057. doi:10.1111/gcb.12195.

Jenouvrier S, Desprez M, Fay R, Barbraud C, Weimerskirch H, Delord K, Caswell H. 2018. Climate change and functional traits affect population dynamics of a long-lived seabird. Journal of Animal Ecology. 87(4):906–920. doi:10.1111/1365-2656.12827.

Jenouvrier S, Holland M, Stroeve J, Barbraud C, Weimerskirch H, Serreze M, Caswell H. 2012. Effects of climate change on an emperor penguin population: analysis of coupled demographic and climate models. Global Change Biology. 18(9):2756–2770. doi:10.1111/j.1365-2486.2012.02744.x.

Jonsson KI. 1997. Capital and incoming breeding as alternative tactics of resource use in reproduction. OIKOS. 78:57–66.

Keogan K, Daunt F, Wanless S, Phillips RA, Walling CA, Agnew P, Ainley DG, Anker-Nilssen T, Ballard G, Barrett RT, et al. 2018. Global phenological insensitivity to shifting ocean temperatures among seabirds. Nature Climate Change. 8(4):313–318. doi:10.1038/s41558-018-0115-z.

Komers PE. 1997. Behavioural plasticity in variable environments. Canadian Journal of Zoology. 75(2):161–169. doi:10.1139/z97-023.

Krüger L, Pereira JM, Paiva VH, Ramos JA. 2019. Personality influences foraging of a seabird under contrasting environmental conditions. Journal of Experimental Marine Biology and Ecology. 516(April):123–131. doi:10.1016/j.jembe.2019.04.003.

Le Bohec C, Durant JM, Gauthier-Clerc M, Stenseth NC, Park YH, Pradel R, Grémillet D, Gendner JP, Le Maho Y. 2008. King penguin population threatened by Southern Ocean warming. Proceedings of the National Academy of Sciences of the United States of America. 105(7):2493–2497. doi:10.1073/pnas.0712031105.

Lecomte VJ, Sorci G, Cornet S, Jaeger A, Faivre B, Arnoux E, Gaillard M, Trouvé C, Besson D, Chastel O, et al. 2010. Patterns of aging in the long-lived wandering albatross. Proceedings of the National Academy of Sciences of the United States of America. 107(14):6370–6375. doi:10.1073/pnas.0911181107.

Lempidakis E, Shepard ELC, Ross AN, Matsumoto S, Koyama S, Takeuchi I, Yoda K. 2022. Pelagic seabirds reduce risk by flying into the eye of the storm. Proceedings of the National Academy of Sciences of the United States of America. 119(41):1–7. doi:10.1073/pnas.2212925119.

Lengagne T. 2008. Traffic noise affects communication behaviour in a breeding anuran, Hyla arborea. Biological Conservation. 141(8):2023–2031. doi:10.1016/j.biocon.2008.05.017.

Lewin PJ, Wynn J, Arcos JM, Austin RE, Blagrove J, Bond S, Carrasco G, Delord K, Fisher-Reeves L, García D, et al. 2024. Climate change drives migratory range shift via individual plasticity in shearwaters. Proc Natl Acad Sci USA. 121(6):e2312438121. doi:10.1073/pnas.2312438121.

Lovenduski NS, Gruber N. 2005. Impact of the Southern Annular Mode on Southern Ocean circulation and biology. Geophysical Research Letters. 32(11):1–4. doi:10.1029/2005GL022727.

Mallory ML, Robinson SA, Hebert CE, Forbes MR. 2010. Seabirds as indicators of aquatic ecosystem conditions: A case for gathering multiple proxies of seabird health. Marine Pollution Bulletin. 60(1):7–12. doi:10.1016/j.marpolbul.2009.08.024.

Marshall GJ. 2003. Trends in the Southern Annular Mode from Observations and Reanalyses. J Climate. 16(24):4134–4143. doi:10.1175/1520-0442(2003)016<4134:TITSAM>2.0.CO;2.

Mathot KJ, Dingemanse NJ. 2012. Animal Personality : Moving Beyond Optimality and Embracing Individual Differences. Integrative Organismal Biology, First Edition.:55–69.

Mazaris AD, Kallimanis AS, Sgardelis SP, Pantis JD. 2008. Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change. Journal of Experimental Marine Biology and Ecology. 367(2):219–226. doi:10.1016/J.JEMBE.2008.09.025.

McClintock BT, Michelot T. 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. Goslee S, editor. Methods in Ecology and Evolution. 9(6):1518–1530. doi:10.1111/2041-210X.12995.

McPhaden MJ, Santoso A, Cai W. 2020. Introduction to El Niño Southern Oscillation in a Changing Climate.

Meuthen D, Baldauf SA, Bakker TCM, Thünken T. 2018. Neglected Patterns of Variation in Phenotypic Plasticity: Age- and Sex-Specific Antipredator Plasticity in a Cichlid Fish. The American Naturalist. 191(4):475–490. doi:10.1086/696264.

Moe B, Frederiksen M, Steen H, Bogdanova MI, Butler A, Wanless S, Moe B, Anker-nilssen T, Frederiksen M, Boulinier T, et al. 2017. Multi-colony tracking reveals spatio-temporal variation in carry-over effects between breeding success and winter movements in a pelagic seabird. Marine Ecology Progress Series. 578(May):167–181.

Montevecchi WA, Regular PM, Rail J-F, Power K, Mooney C, D'Entremont KJN, Garthe S, Guzzwell L, Wilhelm SI. 2021. Ocean heat wave induces breeding failure at the southern breeding limit of the northern gannet Morus bassanus. Marine Ornithology. 49(1).

Moritz C, Agudo R. 2013. The Future of Species Under Climate Change: Resilience or Decline? Science. 341(6145):504–508. doi:10.1126/science.1237190.

National Weather Service - Climate Prediction Center. 2022. Monthly SOI Index. NOAA. [accessed 2022 Jan 20]. https://www.cpc.ncep.noaa.gov/data/indices/soi.

Newell M, Wanless S, Harris M, Daunt F. 2015. Effects of an extreme weather event on seabird breeding success at a North Sea colony. Mar Ecol Prog Ser. 532:257–268. doi:10.3354/meps11329.

Newell RE, Rennie Selkirk, Ebisuzaki W. 1982. The Southern Oscillation: Sea surface temperature and wind relationships in a 100-year data set. Journal of Climatology. 2:357–373. doi:https://doi.org/10.1002/joc.3370020406.

Nourani E, Safi K, de Grissac S, Anderson DJ, Cole NC, Fell A, Grémillet D, Lempidakis E, Lerma M, McKee JL, et al. 2023. Seabird morphology determines operational wind speeds, tolerable maxima, and responses to extremes. Current Biology. 33(6):1179-1184.e3. doi:10.1016/j.cub.2023.01.068.

Nussey DH, Wilson AJ, Brommer JE. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. J of Evolutionary Biology. 20(3):831–844. doi:10.1111/j.1420-9101.2007.01300.x.

Oro D. 2014. Seabirds and climate: knowledge, pitfalls, and opportunities. Front Ecol Evol. 2. doi:10.3389/fevo.2014.00079. http://journal.frontiersin.org/article/10.3389/fevo.2014.00079/abstract.

Orsi AH, Harris U. Fronts of the Antarctic Circumpolar Current - GIS data. https://data.aad.gov.au/metadata/records/antarctic_circumpolar_current_fronts.

Parsons M, Mitchell I, Butler A, Ratcliffe N, Frederiksen M, Foster S, Reid JB. 2008. Seabirds as indicators of the marine environment. ICES Journal of Marine Science. 65(8):1520–1526. doi:10.1093/icesjms/fsn155.

Patrick SC, Charmantier A, Weimerskirch H. 2013. Differences in boldness are repeatable and heritable in a long-lived marine predator. Ecology and Evolution. 3(13):4291–4299. doi:10.1002/ece3.748.

Patrick SC, Weimerskirch H. 2014. Personality, foraging and fitness consequences in a long lived seabird. PLoS ONE. 9(2). doi:10.1371/journal.pone.0087269.

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, et al. 2010. Scenarios for Global Biodiversity in the 21st Century. Science. 330(6010):1496–1501. doi:10.1126/science.1196624.

Pereira JM, Paiva VH, Ceia FR, Ramos JA. 2020. Facing extremes: Cory's shearwaters adjust their foraging behaviour differently in response to contrasting phases of North Atlantic Oscillation. Regional Environmental Change. 20(3). doi:10.1007/s10113-020-01662-1.

Reed TE, Warzybok P, Wilson AJ, Bradley RW, Wanless S, Sydeman WJ. 2009. Timing is everything: flexible phenology and shifting selection in a colonial seabird. Journal of Animal Ecology. 78(2):376–387. doi:10.1111/j.1365-2656.2008.01503.x.

Richardson PL, Wakefield ED, Phillips RA. 2018. Flight speed and performance of the wandering albatross with respect to wind. Movement Ecology. 6(1):3. doi:10.1186/s40462-018-0121-9.

Rogers JC, van Loon H. 1982. Spatial Variability of Sea Level Pressure and 500 mb Height Anomalies over the Southern Hemisphere. Monthly Weather Review. 110(10):1375–1392. doi:https://doi.org/10.1175/1520-0493(1982)110%3C1375:SVOSLP%3E2.0.CO;2.

Salamolard M, Weimerskirch H. 1993. Relationship Between Foraging Effort and Energy Requirement Throughout the Breeding Season in the Wandering Albatross. Functional Ecology. 7(6):643–652. doi:10.2307/2390184.

Santini L, Cornulier T, Bullock JM, Palmer SCF, White SM, Hodgson JA, Bocedi G, Travis JMJ. 2016. A trait-based approach for predicting species responses to environmental change from sparse data: how well might terrestrial mammals track climate change? Global Change Biology. 22(7):2415–2424. doi:10.1111/gcb.13271.

Selwood KE, McGeoch MA, Mac Nally R. 2015. The effects of climate change and land-use change on demographic rates and population viability. Biological Reviews. 90(3):837–853. doi:10.1111/brv.12136.

Shaffer SA, Costa DP, Weimerskirch H. 2003. Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. Functional Ecology. 17(1):66–74. doi:10.1046/j.1365-2435.2003.00705.x.

Shaffer SA, Weimerskirch H, Costa DP. 2001. Functional significance of sexual dimorphism in Wandering Albatrosses, Diomedea exulans. Functional Ecology. 15(2):203–210. doi:10.1046/j.1365-2435.2001.00514.x.

Sharpe LL, Bayter C, Gardner JL. 2021. Too hot to handle? Behavioural plasticity during incubation in a small, Australian passerine. Journal of Thermal Biology. 98:102921. doi:10.1016/j.jtherbio.2021.102921.

Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution. 19(7):372–378. doi:10.1016/j.tree.2004.04.009.

Snell-Rood EC. 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. Animal Behaviour. 85(5):1004–1011. doi:10.1016/j.anbehav.2012.12.031.

Somveille M, Dias MP, Weimerskirch H, Davies TE. 2020. Projected migrations of southern Indian Ocean albatrosses as a response to climate change. Ecography. 43(11):1683–1691. doi:10.1111/ecog.05066.

Speakman CN, Hoskins AJ, Hindell MA, Costa DP, Hartog JR, Hobday AJ, Arnould JPY. 2021. Influence of environmental variation on spatial distribution and habitat-use in a benthic foraging marine predator. Royal Society Open Science. 8(10). doi:10.1098/rsos.211052.

Stamps JA. 2016. Individual differences in behavioural plasticities. Biological Reviews. 91(2):534–567. doi:10.1111/brv.12186.

Stamps JA, Biro PA. 2016. Personality and individual differences in plasticity. Current Opinion in Behavioral Sciences. 12:18–23. doi:10.1016/j.cobeha.2016.08.008.

Stearns SC. 1992. The Evolution of Life Histories. Wiley/Blackwell (10.1111). [accessed 2018 Sep 10]. http://doi.wiley.com/10.1046/j.1420-9101.1993.6020304.x.

Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M. 2002. Ecological effects of climate fluctuations. Science. 297(5585):1292–1296. doi:10.1126/science.1071281.

Thompson DWJ, Wallace JM. 2000. Annular Modes in the Extratropical Circulation. Part I: Month-to-Month Variability*. J Climate. 13(5):1000–1016. doi:10.1175/1520-0442(2000)013<1000:AMITEC>2.0.CO;2.

Thuiller W, Broennimann O, Hughes G, Alkemade JRM, Midgley GuyF, Corsi F. 2006. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. Global Change Biology. 12(3):424–440. doi:10.1111/j.1365-2486.2006.01115.x.

Van De Pol M, Jenouvrier S, Cornelissen JHC, Visser ME. 2017. Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. Phil Trans R Soc B. 372(1723):20160134. doi:10.1098/rstb.2016.0134.

Van de Walle J, Sun R, Fay R, Patrick SC, Barbraud C, Delord K, Weimerkirch H, Jenouvrier S. 2024. The impact of boldness on demographic rates and life-history outcomes in the wandering albatross. Journal of Animal Ecology. 93(6):676–690. doi:10.1111/1365-2656.14077.

Verbeek MEM, Drent PJ, Wiepkema PR. 1994. Consistent individual differences in early exploratory behaviour of male great tits. Animal Behaviour. 48(5):1113–1121. doi:10.1006/anbe.1994.1344.

Volzke S, McMahon CR, Hindell MA, Burton HR, Wotherspoon SJ. 2021. Climate influences on female survival in a declining population of southern elephant seals (Mirounga leonina). Ecology and Evolution. 11(16):11333–11344. doi:10.1002/ece3.7919.

Wakefield ED, Phillips RA, Matthiopoulos J, Fukuda A, Higuchi H, Marshall GJ, Trathan PN. 2009. Wind field and sex constrain the flight speeds of central-place foraging albatrosses. Ecological Monographs. 79(4):663–679. doi:10.1890/07-2111.1.

Wang C, Deser C, Yu J-Y, DiNezio P, Clement A. 2016. El Niño and Southern Oscillation (ENSO): A Review. In: Glynn P, Manzello D, Enochs I, editors. Coral Reefs of the Eastern Tropical Pacific. Vol. 8. http://www.springer.com/series/7539.

Wang G, Cai W, Santoso A, Wu L, Fyfe JC, Yeh SW, Ng B, Yang K, McPhaden MJ. 2022. Future Southern Ocean warming linked to projected ENSO variability. Nature Climate Change. 12(7):649–654. doi:10.1038/s41558-022-01398-2.

Weimerskirch H. 1992. Reproductive Effort in Long-Lived Birds: Age-Specific Patterns of Condition, Reproduction and Survival in the Wandering Albatross. Oikos. 64(3):464. doi:10.2307/3545162.

Weimerskirch H. 2018. Linking demographic processes and foraging ecology in wandering albatross-Conservation implications. Bouwhuis S, editor. Journal of Animal Ecology. 87(4):945–955. doi:10.1111/1365-2656.12817.

Weimerskirch H, Cherel Y, Delord K, Jaeger A, Patrick SC, Riotte-Lambert L. 2014. Lifetime foraging patterns of the wandering albatross: Life on the move! Journal of Experimental Marine Biology and Ecology. 450:68–78. doi:10.1016/j.jembe.2013.10.021.

Weimerskirch H, Collet J, Corbeau A, Pajot A, Hoarau F, Marteau C, Filippi D, Patrick SC. 2020. Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the extent of nondeclared fishing. Proceedings of the National Academy of Sciences. 117(6):3006–3014. doi:10.1073/pnas.1915499117.

Weimerskirch H, Filippi DP, Collet J, Waugh SM, Patrick SC. 2018. Use of radar detectors to track attendance of albatrosses at fishing vessels. Conservation Biology. 32(1):240–245. doi:10.1111/cobi.12965.

Weimerskirch H, Guionnet T. 2002. Comparative activity pattern during foraging of four albatross species. Ibis. 144(1):40–50. doi:10.1046/j.0019-1019.2001.00021.x.

Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. Proceedings of the Royal Society B: Biological Sciences. 267(1455):1869–1874. doi:10.1098/rspb.2000.1223.

Weimerskirch H, Lallemand J, Martin J. 2005. Population sex ratio variation in a monogamous long-lived bird, the wandering albatross. Journal of Animal Ecology. 74(2):285–291. doi:10.1111/j.1365-2656.2005.00922.x.

Weimerskirch H, Louzao M, De Grissac S, Delord K. 2012. Changes in wind pattern alter albatross distribution and life-history traits. Science. 335(6065):211–214. doi:10.1126/science.1210270.

Weimerskirch H, Pinaud D, Pawlowski F, Bost C. 2007. Does Prey Capture Induce Area-Restricted Search? A Fine-Scale Study Using GPS in a Marine Predator, the Wandering Albatross. The American Naturalist. 170(5):734–743. doi:10.1086/522059.

Weimerskirch H, Wilson R, Lys P. 1997. Activity pattern of foraging in the wandering albatross:a marine predator with two modes of prey searching. Mar Ecol Prog Ser. 151:245–254. doi:10.3354/meps151245.

Wilson DS. 1998. Adaptive individual differences within single populations. Philosophical Transactions of the Royal Society B: Biological Sciences. 353(1366):199–205. doi:10.1098/rstb.1998.0202.

Wong BBM, Candolin U. 2015. Behavioral responses to changing environments. Behavioral Ecology. 26(3):665–673. doi:10.1093/beheco/aru183.