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Albatrosses respond adaptively to climate variability by changing variance in a foraging trait

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Abstract

The ability of individuals and populations to adapt to a changing climate is a key determinant of population dynamics. While changes in mean behaviour are well studied, changes in trait variance have been largely ignored, despite being assumed to be crucial for adapting to a changing environment. As the ability to acquire resources is essential to both reproduction and survival, changes in behaviours that maximize resource acquisition should be under selection. Here, using foraging trip duration data collected over 7 years on black-browed albatrosses (*Thalassarche melanophris*) on the Kerguelen Islands in the southern Indian Ocean, we examined the importance of changes in the mean and variance in foraging behaviour, and the associated effects on fitness, in response to the El Niño Southern Oscillation (ENSO). Using double hierarchical models, we found no evidence that individuals change their mean foraging trip duration in response to a changing environment, but found strong evidence of changes in variance. Younger birds showed greater variability in foraging trip duration in poor conditions as did birds with higher fitness. However, during brooding, birds showed greater variability in foraging behaviour under good conditions, suggesting that optimal conditions allow the alteration between chick provisioning and self-maintenance trips. We found weak correlations between sea surface temperature and the ENSO, but stronger links with sea-level pressure. We suggest that variability in behavioural traits affecting resource acquisition is under selection and offers a mechanism by which individuals can adapt to a changing climate. Studies which look only at effects on mean behaviour may underestimate the effects of climate change and fail to consider variance in traits as a key evolutionary force.

KEYWORDS
bet-hedging, intra-individual variability, resource acquisition, salt-water immersion logger, seabirds, Southern Oscillation Index

1 | INTRODUCTION

A major challenge in contemporary ecology is to understand how environmental change impacts individuals, populations and species. Climate is a crucial driver of population dynamics and, as such, has the potential to induce ecosystem-wide changes (Hughes, 2000; Oro, 2014; Stenseth, 2002; Walther, 2002). There are an increasing number of studies demonstrating the effects of broad-scale climate variations on the survival and reproduction across diverse species, but understanding the mechanisms through which these effects emerge is crucial to predict the future consequences of climate change (Oro, 2014; Stenseth, 2002; Walther, 2002). Climate variation is known to alter food webs at large scales (Barber & Chavez, 1983; Chiu-Werner et al., 2019; Sydeman et al., 2015), thought to be driven by changes to local environmental conditions that alter resource availability. As such, changes in resource acquisition may play a key role in driving the widespread climatic effects on species.

Changes in the climate are known to affect prey availability and distribution, particularly in the marine environment (Sydeman et al., 2012), and these are coupled with changes in foraging behaviour. Climate effects can increase foraging trip duration as transit times change due to shifts in food distribution. For example, king penguins (*Aptenodytes patagonicus*) feed extensively at the Antarctic polar front, and El Niño warming events lead to a southerly shift in the front location, associated with an increased trip duration (Bost et al., 2015). Trip durations may also increase as searching times are higher when food is less abundant. In female northern elephant seals (*Mirounga angustirostris*), increased foraging trip durations were observed in an El Niño year and this was coupled with lower foraging success (Crocker et al., 2006). Evidence of decreases in foraging site fidelity under poorer conditions supports the hypothesis that individuals may be forced to visit more foraging patches to obtain sufficient food. One recent study in little penguins (*Eudyptula minor*) examined how site fidelity changed with sea surface temperature (SST), showing that variability in space use was highest under poor conditions, suggesting individuals visit patches that are more dispersed (Carroll et al., 2018). Marginal value theorem predicts that individuals will vary their time in patch as a result of patch quality (Charnov, 1976) and there is evidence from southern elephant seals (*Mirounga leonine*) that dive times were longer in poorer quality patches (Thums et al., 2013), which would likely have knock-on effects for trip duration. This leads to the prediction that animals will vary the time they spend in a patch depending on its quality. This could increase the variability in trip duration, both as a result of lower quality patches or due to patches of less predictable quality. However, two major gaps remain in our knowledge. First, despite the complexity of climatic effects, studies tend to look at single environmental parameters, likely missing other important environmental effects linked to broad-scale climate phenomena. Second, while there have been many studies looking at the consistency in foraging trip duration (reviewed by Ceia & Ramos, 2015) and although often referred to as individual variability, these studies look at a population measure of repeatability in traits and among-individual differences. There has been no attempt to assess intra-individual variability in foraging trip duration, an estimate of variability per individual (Stamps et al., 2012; Westneat et al., 2015). This is surprising as it is key to resource acquisition and known to be more variable and only partly correlated with spatial measures (Harris et al., 2020; e.g. Patrick et al., 2014).

Changes in mean trait values in response to changes in the environment, that is phenotypic plasticity (Charmantier et al., 2008; Dingemanse et al., 2010; Nussey et al., 2005), are reported across behavioural traits. However, while variability in foraging behaviours are likely to be an important mechanism through which individuals mediate the effects of changing prey distributions, studies looking at this are much rarer. This is despite being acknowledged as an important source of ecological variation (Houslay et al., 2019; e.g. Hückstädt et al., 2012; Montiglio et al., 2015) with a heritable component (Martin et al., 2017; Prentice et al., 2020). This is surprising as within-individual variation is required for individuals to adapt to a changing environment and for such phenotypic plasticity to evolve. Studies that have addressed the adaptive nature of changes in trait variability have shown that selection may act to both minimize (Bergmuller & Taborsky, 2010; Johnstone, 2001; Nesse, 2001) and increase (Maynard Smith, 1974; Stamps et al., 2012; Whiten & Byrne, 1997) the residual within-individual variation under different conditions, highlighting that the environment may play a crucial role in the regulation of variation. When environmental conditions are predictable, selection should minimize variability in traits. However, under unpredictable or changing conditions, variability is likely to be adaptive (Seger & Brockmann, 1987). Such variability in foraging trip duration will be under selection as the ability to make longer trips, of more variable duration, will ensure sufficient food can be obtained for the adult and offspring. This will maximize reproductive success and survival probability such that selection will favour individuals that can adapt to a changing climate through shifting the mean and increasing the variance in traits.

The El Niño Southern Oscillation (ENSO) is a leading mode of climate variability and has far-reaching impacts on weather and climate over large portions of the globe, including over the Southern Ocean (Ropelewski & Halpert, 1987). It is known to affect the mean and variability in environmental conditions, such as SST and sea-level pressure (SLP), and that this has knock-on effects on prey abundance and distribution (Deser et al., 2010; Garzke et al., 2015; Perry et al., 2005). The effects on individual environmental parameters are known to be complex and variable over space and time, and hence modelling the phenomena as a whole is important. Capturing changes in foraging behaviour over time requires long-term observations of foraging traits. Seabirds are an ideal bioindicator for such research as the wealth of biologging data can be used to model within- and between-individual changes over time, through repeated measures within and between years. Coupling these data with long-term measures of reproductive success on individual birds is crucial to assessing how selection acts on variability. Variance in foraging strategies has been linked to a variety of factors such as sex (e.g. Bearhop et al., 2006; Kernaléguen et al., 2012; Wright & Radford, 2010), morphology (e.g. van de Pol et al., 2009) and age (Gustafsson,

1988; Votier et al., 2017). Given it is widely acknowledged that when selection acts on subsections of populations, effects on demographic parameters can be amplified and so it is crucial to examine the interaction between intrinsic factors, foraging variability and environmental change.

In this study, we combined long-term biologging data on foraging trip duration (hereafter trip duration), a proxy for foraging effort, with global climate data sets. Salt-water immersion logger data, yielding trip duration, across a 7-year period, were collected on black-browed albatrosses (*Thalassarche melanophris*) breeding in the Subantarctic Kerguelen Islands, and were combined with long-term demographic data on the age, sex and reproductive performance for all individuals. Wide-ranging species, in particular, have been found to exhibit shifts in foraging behaviour in response to climate, a result of their large foraging ranges (Bost et al., 2015; e.g. Crocker et al., 2006) and the highly heterogeneous, patchy environment in which they forage (Weimerskirch, 2007). The increased use of double hierarchical generalized linear mixed models (DHGLMs) in ecology offers a robust statistical tool for quantifying individual differences in both the mean and variability in response to a range of covariates (Cleasby et al., 2015). Here, using DHGLMs, we quantified the effects of ENSO, as measured by the Southern Oscillation Index (SOI) on trip duration, linked to age and sex and within different breeding stages. Finally, we demonstrated how our results link to small changes in both mean and variance of SST, which is regularly studied in relation to seabird behaviour, and found more pronounced effects in the rarely studied SLP.

2 | METHODS

2.1 | Study species

This study was conducted at Cañon de Sourcils Noirs, Kerguelen Islands (49.7°S, 70.2°E). Black-browed albatrosses are annual breeders, with strong monogamous pair bonds. Breeding begins in October, with chicks hatching in late December. The pair shares both incubation (period duration = 70 days) and chick brooding (hereafter brooding; period duration = 21 days) roles. Following the brooding stage, they continue to provision the chick, until mid-April, when all chicks have fledged. As part of a long-term monitoring program, nests are checked to identify ringed individuals and monitor breeding success at (i) the start of incubation to record breeding attempts; (ii) during hatching to measure hatching success; and (iii) at the end of the season to record fledging success. Throughout the manuscript, reproductive success is defined as successfully fledging a chick. These measures have been recorded annually at this colony since 1979, and all adults and chicks in the study population are ringed with a unique metal band enabling the estimation of age. For birds born in the population, exact birth dates are known; for immigrant birds age is estimated as the date at first breeding—7 years (mean age at first reproduction). Birds are sexed genetically or based on structural size, with males being slightly larger. Fledging success was

used as a proxy of individual quality with birds divided into successful and unsuccessful breeders based on the reproductive success in the relevant season. For this study, incubation and brooding periods were considered separately as birds visit different areas and have different constraints on their behaviour.

2.2 | Foraging trip duration

2.2.1 | Data collection

From 2006 to 2013, adult breeding black-browed albatrosses were equipped with GLS Geolocation-immersion logger (British Antarctic Survey; Mk4, Mk5, Mk9, Mk15, Mk19 models) and Mk3006 (Biotrack/Lotek®), weighing 5 g (Mk4), 3.6 g (Mk5) or 2.5 g (other models), which is 0.07%–0.14% of the adult body mass (Desprez et al., 2018). Birds were caught on the nest and devices were attached to plastic rings which were fitted on the leg. For this study, we used data from the salt-water immersion loggers, which detect when the bird is on the water—that is, the logger is immersed in salt water. Mk4, Mk5, Mk9, Mk15 and Mk3006 loggers record the proportion of each 10-min interval the electrodes are immersed and Mk19 record the actual duration of immersion. In total, 94 birds were equipped with 153 GLS (51 birds × 1; 28 birds × 2; 14 birds × 3; 1 bird × 4) and loggers were left on for between 1 and 4 years. In total, this yielded 167 birds (94 tracked individuals and 73 partners of known identity), where we had an estimate of foraging trip duration, breeding success, age and sex.

2.2.2 | Data processing

When foraging at sea, birds alternate periods in flight (logger records = 'Dry') and periods on the water ('Wet', the feet and lower leg of the bird carrying the GLS is in the salt water, producing a contact between two electrodes). 'Wet' periods on the water last between a few seconds to a maximum of 12 h, demonstrating the bird is at sea. 'Dry' periods of <7 h are indicative of flight (Maximum continuous flight time; Desprez et al., 2018). 'Dry' periods greater >7 ho are therefore when the bird is on the land. The start of the foraging trip is thus measured as the first 'Wet' event immediately after a 'Dry' period >7 ho, and the end of this trip as the last 'Wet' event immediately before the first 'Dry' period >7 h. The duration of this period is defined as the foraging trip duration (hereafter trip duration; Desprez et al., 2018). In this study, only incubation and brooding periods were considered as after the chick is left alone, it is not possible to accurately assess trip duration as periods on land can be very short and hence not distinguishable from flight. Once the trip duration of the equipped bird was estimated, the trip duration of partners could also be estimated, that is the time the equipped bird was on the nest. The first observation of the equipped bird was always on the nest, as loggers were deployed here, such that there are more trip duration estimations for partners than equipped birds.

2.3 | Climate metrics

2.3.1 | Data acquisition and processing

While traditionally associated with warmer SST and lower productivity in the eastern tropical Pacific, studies have shown that climatic effects of El Niño are complex and often lead to cooler waters in other regions around the globe (Hermes & Reason, 2005; Reason et al., 2000; Subramaniam et al., 2020). For example, some areas exhibit colder SST and/or higher productivity in El Niño years, whereas others show lagged effects to El Niño-associated cooling, often linked to bathymetric features and front locations. Despite this complexity, there is strong evidence that ENSO has important impacts on marine species, driving changes in fitness and population dynamics (Cubaynes et al., 2011; Oro, 2014; Oro et al., 2013). At this colony on the Kerguelen Islands, evidence suggests that El Niño years are actually optimal for reproductive success (Nevoux et al., 2010; Wilson & Adamec, 2002) and hence this classifies the 'good' versus 'poor' foraging conditions we use in the paper, with the latter occurring in conjunction with La Niña events. We analysed environmental conditions during the pre-breeding (August–October) and breeding season (December–February) during the period 2008–2018. First, monthly measures of SOI strength from National Oceanic and Atmospheric Administration (https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/) for each year were averaged for August, September and October prior to the commencement of breeding (November) per year to obtain an estimate of SOI conditions during the pre-breeding period. We used the SOI measures for this period, as these have previously been shown to have the strongest effect on reproductive success (Desprez et al., 2018). This value for pre-breeding SOI was fitted in all models assessing how the environment affected trip duration.

Second, to help understand the mechanism through which ENSO may affect trip duration, we examined the effect of SOI on two environmental variables—SLP and SST. The SOI defines ENSO events as changes in SLP across the Indo-Pacific. SLP also captures global atmospheric circulation changes in large-scale pressure and wind patterns during ENSO events and thus mediates ENSO's impacts from the tropical Pacific to the extratropics in both hemispheres (Taschetto et al., 2020). Therefore, we examined SLP as an intermediate measure of ENSO at a regional scale, where it can have local effects on SST around the broader Kerguelen region. Monthly gridded fields from the following observational and reanalysis products were used in this assessment: SLP at 2.5° horizontal resolution from the National Centers for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR; Kistler et al., 2001) and NOAA Optimum Interpolation SST v2 (Reynolds et al., 2002) at 1° horizontal resolution. The analysis period was taken as March 2008–February 2018, and the focus was on the austral summer months for incubation period (December) and brooding period (January–February). For both incubation and brooding period, we calculated long-term mean environmental conditions (i.e. the average conditions for SLP and SST for all years
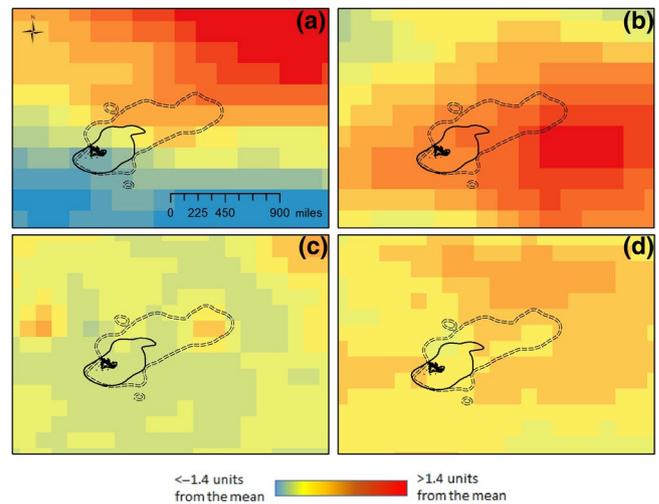

FIGURE 1 Deviation from the mean sea-level pressure (SLP; a and b) and sea surface temperature (SST; c and d) under El Niño (low SOI; a and c) and La Niña (high SOI; b and d). Maps show SLP and SST for December (incubation) here, as the values change little during brooding (January/February). The foraging range for both incubation (double dashed lines) and brooding (January/February; single solid line) are plotted as it is predominantly the shift in foraging area that drives changes in the environment between these periods. Maps showing the SLP and SST anomalies for both brooding and incubation can be found in the Supporting Information Appendix 2 (Figures S1–S4)

in the analysis period). To determine unusual environmental conditions during ENSO years, we selected years that were formally classified by the NOAA Climate Prediction Center as exhibiting ENSO conditions during the August–October period prior to starting breeding. We defined El Niño or La Niña conditions to exist when the 3-month SST anomaly average in the equatorial Pacific region (5°N–5°S, 120°–170°W) exceeded +/-0.4°C. During the analysis period March 2008 to February 2018, the following years were identified as exhibiting El Niño conditions (i.e. low SOI): 2009/2010 and 2015/2016; the following as La Niña conditions (i.e. high SOI): 2010/2011, 2011/2012, 2016/2017 and 2017/2018. All other years were classified as 'normal' (i.e. neither exhibiting El Niño nor La Niña conditions). We extended the SOI analysis period beyond that of the foraging trip study period to have the best estimate of how SOI affects the environment and averaged across years to obtain the most robust estimates of environmental conditions. For those years, identified as exhibiting El Niño and La Niña conditions, average SLP and SST conditions during the incubation (December) and brooding season (January–February), were generated and used in the foraging trip analyses (Figure 1). Henceforth, the terminology 'poor' and 'good' conditions are used to reflect environmental conditions encountered by the black-browed albatross regionally around Kerguelen and coinciding with La Niña and El Niño events respectively. In addition, to better emphasize the deviations in SST and SLP during ENSO years relative to long-term mean conditions, Figures S1 and S2 also show anomalies in SLP and SST relative to all years. Intra-event variance in SST and SLP for ENSO years (Figures

S3 and S4) highlights how variable environmental conditions are among El Niño and La Niña years respectively.

In order to link SOI and local environmental conditions for the colony, we estimated the foraging range of albatrosses using GPS tracking data from a previous study. We estimated the 95% kernel limit as a measure of foraging range, conducted separately for the incubation and brooding period in ArcGIS 10.4. We then randomly selected 100 locations within those foraging ranges. An estimate of SST and SLP was extracted at each of the 100 random locations for both the incubation and brooding period, for high and low SOI years, giving a total of 800 environmental estimates.

2.4 | Statistical analyses

2.4.1 | Trip duration

In order to quantify the effect of climate and life-history traits on the mean and variance on trip duration, we used a double hierarchical DHGLMs. The DHGLM allows for the simultaneous analysis of a mean-level model and a dispersion (variance)-level model each including fixed and random effects. We fitted the same model on both the mean and the dispersion as this was in keeping with our biological predictions that not only the mean foraging trip duration but also the variation in foraging trip was affected by individual and environmental effects. Log-transformed trip duration was fitted as the response variable and the following fixed effects were fitted on both the mean and the variance part of the model: sex, age, breeding stage, reproductive success and their interactions with SOI. Given the complexity of the model, no further interactions were fitted. All non-significant interactions, where parameter estimates overlapped zero, were dropped from the final models (see Table S1 for full model results). Bird identity and year were fitted as random effects on the mean and variance including a covariance between the mean and variance part of the model.

All models were fitted in a Bayesian framework using JAGS (Plummer, 2003) within R version 3.5.2 (R. Development Core Team, 2018) via the package runjags version 2.0.4-2 (Denwood, 2016). DHGLMs were fitted modelling the log of the variances (Hill & Mulder, 2010) and not the log of the standard deviations. We used weak priors on all parameters to avoid biasing parameter estimates. We used a normal distribution with mean of 0 and a precision (1/variance) of 0.001 for fixed effects in both the mean and dispersion part of the model. We used an inverse Wishart prior to an identity matrix as the scale matrix and 5 and 10 *df* for bird identity and year respectively. All models were fitted using three chains each with 1,010,000 iterations, 10,000 burn-in iterations and a thinning interval of 1000. Convergence was first assessed by visually inspecting the trace plots, which were also used to identify an appropriate number of burn-in iterations. We then checked that the Monte Carlo error was less than 1%–5% of the posterior standard deviation, that the Brooks–Gelman–Rubin diagnostic converged to 1 ± 0.2 and that the autocorrelation was below 0.05 for all parameters (Gilks et al.,

1996). The posterior mode and 95% highest posterior density intervals were used to summarize the posterior distributions of the model parameters. Using half-Cauchy and lkj priors on the variance matrix yielded similar results.

2.4.2 | Climate metrics

Changes in the mean and variance in SST and SLP were estimated using the lme function in the nlme (Pinheiro et al., 2021) package in R 3.5 (R. Development Core Team, 2018). Linear mixed models of SST and SLP were fitted with a two-level category for SOI (low—El Niño/high—La Niña) breeding stage (incubation/brooding) and their interaction as fixed effects. A random intercept of location was included to account for repeated measures at each of randomly generated sampling points. A heterogeneous variance structure was fitted using the varIdent option, fitting a variance for each breeding stage and SOI level (i.e. four levels). The fixed effect structure was then assessed by ANOVA type III sums of squares, based on maximum likelihood estimation. The variance structure was assessed by comparing models with and without the heterogeneous variance structure, using a log-likelihood ratio test based on the restricted maximum likelihood estimation.

3 | RESULTS

3.1 | Foraging trip duration

Males and successful breeders made shorter trips and birds made shorter trips during brooding compared to incubation, findings that support previously published work (Table 1). Successful breeders and younger breeders made more variable trips. SOI strongly affected the variability in trip duration and there was a significant effect of SOI on the variability in trip duration dependent on the breeding stage (Figure 2a; Table 1). During brooding, birds showed a strong decrease in variability with increasing SOI, but little change during incubation (Figure 2a). The results showed that during low SOI (good conditions), brooding trips were more variable, but during high SOI (poor conditions), there was little difference between the variability during incubation and brooding. Results show that successful breeders increased their variability in trip duration with increasing SOI, that is when conditions became unfavourable, whereas failed breeders showed little change (Figure 2b; Table 1). As such, the difference in variability was predominantly seen under high SOI (poor conditions). Young birds showed an increase in variability in trip duration with increasing SOI, whereas older birds showed a slight decline (Figure 2c; Table 1) and again the major difference in variability with age was seen under high SOI conditions (poor conditions).

Individual explained a small proportion of the differences in mean trip duration, but a substantial component of individual variance (Table 1). There was a negative covariance between the mean and variance such that birds with longer trips have less variable trips.

TABLE 1 Parameter estimates from model of the effect of Southern Oscillation Index (SOI), age, sex, breeding stage and breeding success on trip duration. Estimates are from a double hierarchical generalized linear mixed model and show the median and the 95% confidence intervals. Significant parameters, where the confidence interval does not overlap with zero, are shown in bold. Non-significant interactions were dropped from the model (for full model with all interactions, see Table S1)

	2.50%	Median	97.5%
Fixed effect structure			
Mean part			
Intercept	**0.68**	**0.98**	**1.22**
Sex (male)	**−0.16**	**−0.10**	**−0.02**
Age	−0.05	−0.02	0.03
Stage (brooding)	**−1.52**	**−1.46**	**−1.40**
Reproductive success (successful)	**−0.19**	**−0.12**	**−0.01**
SOI	−0.30	0.02	0.32
Variance part			
Intercept	**−2.08**	**−1.70**	**−1.30**
Sex (male)	−0.21	−0.07	0.17
Age	**−0.21**	**−0.12**	**−0.03**
Stage (brooding)	−0.05	0.13	0.30
Reproductive success (successful)	**0.21**	**0.45**	**0.70**
SOI	−0.34	0.03	0.48
SOI × Age	**−0.21**	**−0.12**	**−0.03**
SOI × Stage	**−0.46**	**−0.28**	**−0.09**
SOI × RS	**0.07**	**0.31**	**0.56**
Random effect structure			
Individual mean part	**0.05**	**0.07**	**0.08**
Individual mean – Variance covariance	**−0.63**	**−0.44**	**−0.25**
Individual variance part	**0.22**	**0.33**	**0.43**
Year Mean part	**0.03**	**0.07**	**0.19**
Year Mean – Variance covariance	−0.45	0.02	0.56
Year Variance part	**0.04**	**0.08**	**0.24**

This supports evidence that individuals who are successful have shorter and more variable trips. There was an effect of year on both the mean and variance in trip duration, but there was no significant covariance between these (Table 1).

3.2 | Relation between global and localized environmental measures

Mean SST was lower during brooding ($\chi^2_1 = 40.82$; $p < 0.001$) and for low SOI (good conditions) years ($\chi^2_1 = 102.96$; $p < 0.001$), but there was no significant interaction between the breeding stage and SOI ($\chi^2_1 = 1.15$; $p = 0.28$; Figures 1 and 3). There was a significant

interaction between the breeding stage and SOI conditions for the variance in SST (LRT$_3$ = 32.26; $p < 0.001$; Figures 1 and 3). SST was more variable under high SOI (poor conditions), particularly during incubation (Figures 1 and 3).

There was a significant interaction between the breeding stage and SOI conditions for both mean SLP ($\chi^2_1 = 1460.6$; $p < 0.001$) and the variance in SLP (LRT$_3$ = 88.28; $p < 0.001$; Figures 1 and 3). SLP was considerably lower under low SOI (good conditions) than that under high SOI (poor conditions), and lower during brooding than during incubation (Figures 1 and 3). High SOI (poor conditions) was associated with slightly lower variability in SLP (Figures 2 and 3), and more variable SLP during incubation than brooding (Figures 1 and 3).

4 | DISCUSSION

In this study, we examine the effect of ENSO, a global climate phenomenon known to be an important driver of ecosystem-wide changes in the Southern Ocean, on the foraging behaviour of black-browed albatrosses. Our results show that ENSO has a strong impact on the variability in foraging trip duration, with little to no effect on the mean trip duration. This work builds on previous studies which have shown that climate indices can affect diet and between-individual differences in foraging traits (Avalos et al., 2017; Chiu-Werner et al., 2019; e.g. Paiva et al., 2009). Our study demonstrates that ENSO directly affects the variance in individual trip duration at both population and individual level. We believe this is the first evidence that climate-driven changes in foraging trip duration are evident as variability in traits, and failure of previous studies to quantify this may have underestimated the impact of climate change. Furthermore, by combining data on age, sex, breeding stage and individual quality, we also demonstrate that life-history traits mediate the relationship with climate. We demonstrate that global ENSO effects show some limited links with the mean and variance of widely studied SST and larger effects on SLP, which is not commonly linked to foraging trip duration. These results suggest that ENSO may drive changes in foraging behaviour through regional modulation of SST and SLP, but the magnitude of these effects suggests there may be other important environmental and biological drivers to be considered.

While studies usually link ENSO to warmer and less productive waters in the eastern equatorial Pacific, evidence suggests that around our study site El Niño years are associated with cooler, more productive waters and higher reproductive success (Nevoux et al., 2010; Wilson & Adamec, 2002). Our results here support that La Niña years are associated with higher and more variable SST. In contrast under good environmental conditions, as indicated by a low SOI reflecting El Niño years, individuals generally display low variability in foraging behaviour, supporting our original hypothesis. However, when considering incubation and brooding phases separately, there was strong evidence that brooding trip duration became less variable with increasing SOI/La Niña, while incubation trips indicated little change. This showed that it was under good conditions that
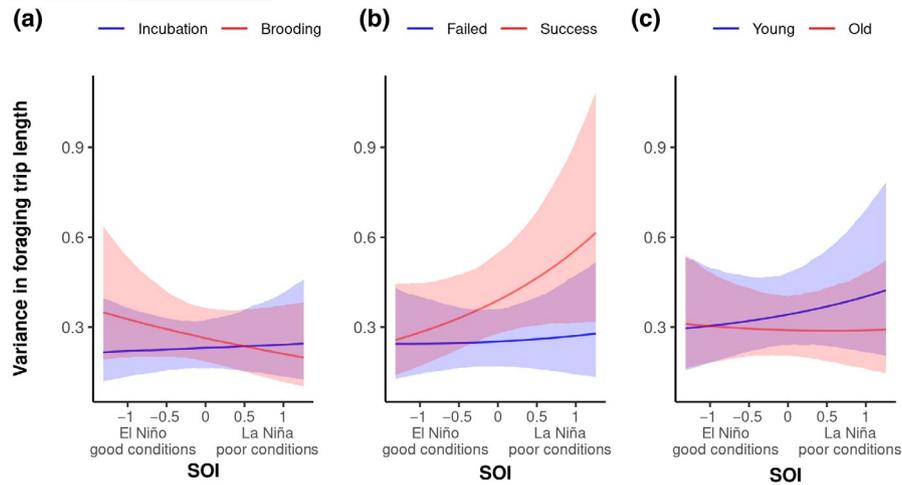
FIGURE 2 The effect of the Southern Oscillation Index (SOI) on the variability in trip duration. El Niño (low SOI) and La Niña (high SOI). (a) The interaction between SOI and breeding stage on the variability in trip duration. (b) The interaction between SOI and reproductive performance on the variability in trip duration. (c) The interaction between SOI and age on the variability in trip duration. Age was fitted as a continuous variable, but for graphical purpose, we used 10 and 26 years old for young and old birds which are the 10% and 90% quantile of age ranging from 5 to 46 years old
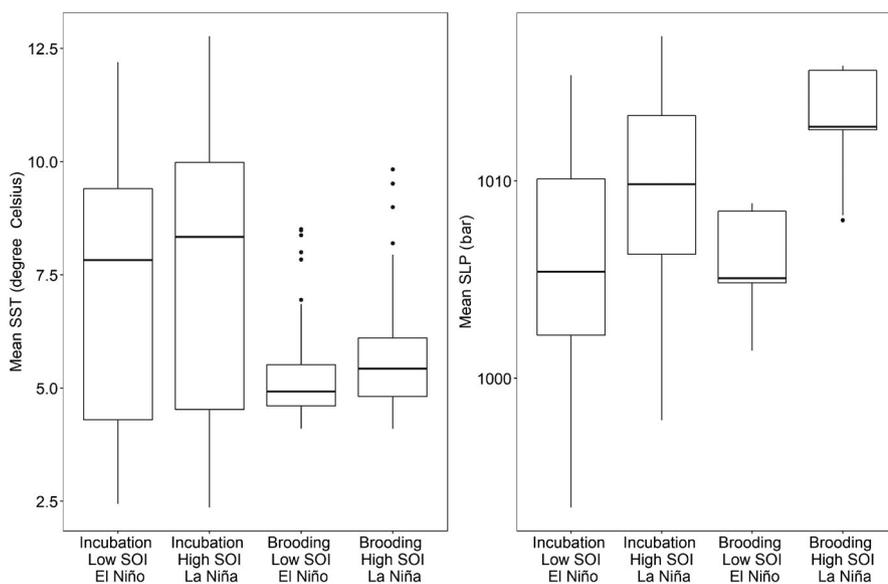
FIGURE 3 The mean and variance in (a) sea surface temperature (SST) and (b) mean sea-level pressure (SLP) between incubation (December) and brooding (January/February) periods in El Niño (Low SOI) and La Niña (High SOI) years. Differences in conditions between breeding stages are driven mainly by a change in the foraging area (see Figure 1). SOI, Southern Oscillation Index

brooding and incubation trips differed most, and under good conditions that brooding behaviour was most variable. When environmental conditions are favourable, it is possible that chicks are in good condition and hence resilient to more variable periods without food. This would enable adults to acquire more resources for self-maintenance when necessary and as self-maintenance trips are longer, this would increase the variability in trip duration. Brooding is the most energetically demanding period for adult birds and so under poor conditions they may have little opportunity to conduct longer trips to more profitable areas or prioritize their own body condition. Furthermore, during brooding birds forage in a small area around the Kerguelen shelf edge, whereas during incubation they range much more widely, in more diverse habitats and this spatial difference could lead to differential effects to ENSO.

Overall, under poor conditions, high SOI/La Niña years, successful breeders increased their variability in foraging trip duration, demonstrating that such a change appears to be adaptive. Our results suggest it is the individuals that display higher variability in foraging trip duration that are able to overcome the constraints imposed by poorer conditions and adapt to less favourable conditions and that variability in trip duration is linked to a range of life-history traits. Younger birds show a stronger increase in variability with high SOI/La Niña than old birds, which suggests they are better able to adapt to the environmental change. Evidence of declines in reproductive success with age have been found in many species, including this population of black-browed albatrosses (Pardo et al., 2013). A failure to increase variability when the conditions warrant it could provide a mechanism through which senescence occurs. Our results on mean trip duration show that sex

differences in trip duration are consistent with well-reported findings that male black-browed albatrosses often make shorter trips, as well as all birds during brooding (Patrick & Weimerskirch, 2014a; 2014b; Phillips et al., 2004; Weimerskirch et al., 1993).

The recent increase in studies looking at intra-individual variability in behaviour has allowed researchers to improve their understanding of the biological significance of these differences (Mitchell et al., 2021; Westneat et al., 2015). Any trait that changes along a gradient will show variability. The increase in the use of behavioural reaction norms (Dingemanse et al., 2010) has demonstrated that such variability may be plastic in response to a measured covariate. In our study, the variability we see may well represent an adaptive change to unmeasured environmental parameters. While ideally a study would measure all possible drivers of behavioural change, this is near impossible in the wild. DHGLMs allow us to capture this variation without needing to have information about all possible environmental effects. They also allow residual variation, sometimes referred to as intra-individual variability (Stamps et al., 2012), to be quantified. Residual variation may be a trait in itself, but it is difficult to partition unmeasured plasticity for genuine variability (Westneat et al., 2015). However, here we demonstrate that this residual variability changes with the environment and that this is adaptive in our study species, highlighting its importance for adaptation in the wild.

Observations, theory and climate models suggest that variability in the environment is likely to increase with global climate change, including changes in extreme events (Ummenhofer & Meehl, 2017). Our study suggests that higher quality individuals (those with higher reproductive success) and younger birds will be best equipped to adapt to such changes in climate, and that if individual variability is under selection, the variability in trip duration itself may increase over time. The relatively small, though detectable, effects of ENSO on SST near our colony, and the inclusion of SLP differences, highlight the importance of using environmental parameters that capture small- and large-scale processes over varying temporal scales and highlight the power of broad-scale climate indices to capture this variation.

Evidence for an effect of climate variation on foraging behaviour is mixed (Avalos et al., 2017; Paiva et al., 2009). Our study demonstrates that a failure to examine the effects on the variance in traits and the use of single environmental parameters, assumed to be important across sites and species, will underestimate and potentially mask critical impacts of climate changes. This study suggests that high variability can be adaptive in a changing climate, but we do not know if the variability has a genetic basis and we cannot predict whether birds would be able to optimize their behaviour over their lifetime rapidly enough to adapt to the increasing number of extreme events. Given subsections of the population, and different biological stages, show different levels of variability, if conditions deteriorate, favouring high variability, important components of the population may be lost, such as older individuals or a single sex, which would weaken the persistence of the population. Similarly, populations that differ in age and sex structure will on average respond differently to changes in the environment. Given the increasing evidence that within-individual variability in traits is crucial to predict the ability of populations to adapt to a changing climate, our results present a robust test of the importance of both mean and variance in foraging behaviour in a long-lived seabird. We also demonstrate that the majority of climate effects are seen on the variability in foraging behaviour and hence failure to account for these effects will mask important effects of the climate on behaviour.

AUTHOR CONTRIBUTION

Samantha C. Patrick, Julien G. A. Martin and Henri Weimerskirch conceived the study. Samantha C. Patrick, Julien G. A. Martin, Caroline C. Ummenhofer and Alexandre Corbeau analysed the data. Samantha C. Patrick, Alexandre Corbeau and Henri Weimerskirch collected the data. Samantha C. Patrick wrote the manuscript, which was edited by Julien G. A. Martin, Caroline C. Ummenhofer, Henri Weimerskirch and Alexandre Corbeau. All the authors contributed to the revising of the final version of this manuscript.

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SUPPORTING INFORMATION

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