

RESEARCH ARTICLE

Linking oceanographic conditions, migratory schedules and foraging behaviour during the non-breeding season to reproductive performance in a long-lived seabird

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Abstract

1. Studies of the mechanisms underlying climate-induced population changes are critically needed to better understand and accurately predict population responses to climate change. Long-lived migratory species might be particularly vulnerable to climate change as they are constrained by different climate conditions and energetic requirements during the breeding and non-breeding seasons. Yet, most studies primarily focus on the breeding season of these species life cycle. Environmental conditions experienced in the non-breeding season may have downstream effects on the other stages of the annual life cycle. Not investigating such effects may potentially lead to erroneous inferences about population dynamics.
2. Combining demographic and tracking data collected between 2006 and 2013 at Kerguelen Island on a long-lived migratory seabird, the Black-Browed Albatross (*Thalassarche melanophris*), we investigated the links between sea surface temperature during the non-breeding season and behavioural and phenological traits (at-sea behaviour and migratory schedules) while accounting for different responses between birds of different sex and reproductive status (previously failed or successful breeders). We then explored whether variation in the foraging behaviour and timing of spring migration influenced subsequent reproductive performance.
3. Our results showed that foraging activity and migratory schedules varied by both sex and reproductive status suggesting different energetic requirements and constraints among individuals. Higher sea surface temperatures during late winter, assumed to reflect poor winter conditions, were associated with an earlier departure from the wintering grounds and an extended pre-breeding period. However, an earlier spring migration and an earlier return to Kerguelen grounds were associated with a lower breeding success.
4. Our results highlighted that behaviour during some periods of the non-breeding season, particularly towards the end of the wintering period and the pre-breeding period, had a significant effect on the subsequent reproductive success. Therefore,

caution needs to be given to all stages of the annual cycle when predicting the influence of climate on population dynamics.

KEY WORDS

carry-over effect, migration, phenology, protandry, reproductive performance, sea surface temperature, sex, *Thalassarche melanophris*

1 | INTRODUCTION

There is ample evidence that the Earth's climate is changing and impacting species population size and persistence (Barbraud et al., 2012; Root et al., 2003; Sydeman, Poloczanska, Reed, & Thompson, 2015; Thomas et al., 2004). A growing body of work in terrestrial mammals and birds has provided some insights into the mechanisms underlying these population changes by linking climate conditions to resource availability, phenology, body condition, individual fitness traits and population dynamics (Both, Bouwhuis, Lessells, & Visser, 2006; Møller, Rubolini, & Lehikoinen, 2008; Ozgul et al., 2010; Plard et al., 2014; Post & Forchhammer, 2008; Reed, Jenouvrier, & Visser, 2013). Yet, in marine species, although several studies have successfully linked fitness traits to climatic variables (Constable et al., 2014; Jenouvrier, 2013), underlying mechanisms remain particularly challenging to study. However, investigating responses to variability in oceanographic conditions is an important step to predict the consequences of climate on population dynamics of marine species. Climate change impacts marine species mostly indirectly (Sydeman et al., 2015) by operating primarily via changes in the availability of feeding and breeding habitats (Emmerson & Southwell, 2008; Fuentes, Limpus, Hamann, & Dawson, 2010; Hsieh, Kim, Watson, Di Lorenzo, & Sugihara, 2009; Idjadi & Edmunds, 2006; Jones, McCormick, Srinivasan, & Eagle, 2004) and in the productivity and structure of food webs (Carroll et al., 2015; Edwards & Richardson, 2004; Forcada, Trathan, Reid, & Murphy, 2005; Greene, Pershing, Kenney, & Jossi, 2003; Jenouvrier, Péron, & Weimerskirch, 2015; Ramírez et al., 2016; Richardson & Schoeman, 2004), although direct impacts, such as physiological impacts, have also been reported (Reid et al., 2007).

Plasticity in behaviour, physiology and/or morphology provides the potential for individuals to respond rapidly and effectively to environmental changes (Jenouvrier & Visser, 2011; Sydeman et al., 2015). Specifically, plasticity in foraging strategies may allow individuals to compensate for environmental changes induced by climate change. Weimerskirch, Louzao, de Grissac, and Delord (2012) showed that the foraging range of female wandering albatrosses (*Diomedea exulans*) during the breeding season moved southward as a response of a poleward shift of the westerly winds. This adjustment in behaviour coincided with higher breeding success, suggesting that foraging performance may be a key link between environmental changes and vital rates. Yet, the mechanisms by which variation in environmental conditions affects foraging behaviour and subsequently demographic parameters have only recently started to

be explored and studies have mostly been focusing on the breeding season of the individual life cycle (Jenouvrier et al., 2015; Kowalczyk, Reina, Preston, & Chiaradia, 2015; Sarau, Chiaradia, Salton, Dann, & Viblanc, 2016; Weimerskirch et al., 2012).

Migratory marine species use several habitats during their biological cycle and are constrained by different climate conditions and energetic requirements during the breeding and non-breeding seasons. Investigating the impact of climate fluctuations on the breeding part of the life cycle only may therefore lead to incomplete inferences about the population responses to climate change (Ådahl, Lundberg, & Jonzén, 2006; Small-Lorenz, Culp, Ryder, Will, & Marra, 2013). Indeed, individual foraging performance and life-history traits may be more sensitive to the environmental conditions experienced in one particular season (Daunt et al., 2014).

Notably, evidence has been accumulating that environmental conditions during the non-breeding season may have a significant carry-over effect on the reproductive performance of various species (Authier, Dragon, Richard, Cherel, & Guinet, 2012; Norris, Marra, Kyser, Sherry, & Ratcliffe, 2004; van de Pol et al., 2010). Recently, a few studies have also related foraging behaviour during the non-breeding period to subsequent breeding performance. In the migratory Manx shearwaters (*Puffinus puffinus*), birds with low winter foraging activity were more likely to hatch a chick successfully the following season, whereas birds with high activity were more likely to skip breeding (Shoji et al., 2015). Similarly, shorter foraging times in the late winter were associated with earlier and more successful breeding in the European shags (*Phalacrocorax aristotelis*) (Daunt et al., 2014). To our knowledge, only one study has examined the associations between climatic conditions during the non-breeding season, at-sea behaviour and subsequent breeding outcome in a seabird species (European shag: Daunt et al., 2014).

Here, we investigated how climatic conditions during the non-breeding season affected the foraging behaviour of a long-lived migratory seabird, the black-browed albatross (*Thalassarche melanophris*) at Kerguelen Island, and link with subsequent breeding performance. In this albatross population, previous demographic studies have found that an increase in the sea surface temperature (SST) in the north-east and south-east regions of the peri-insular Kerguelen shelf, where this population of albatross is known to forage during the summer (Pinaud & Weimerskirch, 2002), is associated with an increase in breeding success (Nevoux, Weimerskirch, & Barbraud, 2007; Pinaud & Weimerskirch, 2002; Rolland, Barbraud, & Weimerskirch, 2008). Furthermore, the birds' reproductive success has been related to the summer foraging behaviour (Patrick

& Weimerskirch, 2014a, 2014b, 2017), but knowledge outside the breeding season is scarce. Although Rolland et al. (2008) and Nevoux, Forcada, Barbraud, Croxall, and Weimerskirch (2010) found a negative effect of SST around Tasmania during the non-breeding season on breeding success, little is known about non-breeding foraging behaviour and how it may influence future breeding. To fill this gap and to investigate the links between SST, migration schedules, foraging behaviour and demography in a marine migratory species, we combined demographic data from a long-term longitudinal mark-recapture study and tracking data of albatrosses from Kerguelen Island during eight non-breeding seasons (2006–2013).

Previous studies on black-browed albatrosses at South Georgia found an earlier return date to colonies in males than in females and differences in outward migration according to reproductive status and sex (Phillips, Silk, Croxall, Afanasyev, & Bennett, 2005; Tickell & Pinder, 1975). Thus, we first expect foraging behaviour and timing of migration to differ between sexes and individual reproductive status (i.e. if the birds have bred successfully or not in the previous breeding season).

Previous demographic studies on black-browed albatrosses from Kerguelen found positive effects of SST on breeding success around Kerguelen during the breeding season and negative effects of SST around Tasmania during the non-breeding season (Nevoux et al., 2007, 2010; Pinaud & Weimerskirch, 2002; Rolland et al., 2008). Because the effect of SST on the breeding success is probably mediated through the availability and acquisition of resources, we expect that SST affects the foraging activity. In addition, we expect that the foraging activity during the non-breeding and pre-breeding seasons and the timing of the spring migration ultimately influence the individual reproductive performance. Finally, as theoretical and empirical studies have demonstrated fitness advantages of an early return to the breeding colony in migratory birds (Kokko, 1999), we predicted a negative relationship between the return date to the breeding grounds and the breeding success.

2 | MATERIALS AND METHODS

2.1 | Study site and field protocol

The study was carried out at Canyon des Sourcils Noirs (49.4°S, 70.1°E), Kerguelen Islands, Southern Indian Ocean, where a study colony of ~200 nests has been monitored each breeding season with a constant monitoring effort since the 1978/1979 breeding season. From 2006 to 2013, during the breeding season (October–March), breeding adults (incubating, brooding or rearing a chick) were fitted with a GLS (global location sensor) Geolocation-immersion logger (Mk4, Mk5, Mk9, Mk15, Mk19 models; British Antarctic Survey, Cambridge, UK) and Mk3006 (Biotrack/Lotek®), weighing 5 g (Mk4), 3.6 g (Mk5) or 2.5 g (other models), attached to a plastic leg band. The logger and band corresponded to ~0.07%–0.14% of the adult body mass. During the following breeding seasons, the equipped birds were recaptured and the loggers removed. Each year, the breeding success of each individual was recorded as part of the

long-term monitoring of the population. Breeding success was defined as a binary variable: 1 = chick survived to fledging; 0 = egg or chick did not survive. Birds were sexed from blood samples collected following GLS recovery and using standard protocol described in Angelier, Weimerskirch, Dano, and Chastel (2007).

2.2 | Geolocator data and processing

Global location sensor record light measurements allowing the calculation of latitude and longitude except during 2 or 3 weeks around the equinoxes, when only an estimation of longitude is reliable. GLS light data were analysed following Phillips, Silk, Croxall, Afanasyev, and Briggs (2004). To estimate the dates of departure from the breeding colony and of arrival to the non-breeding grounds, we plotted the coordinates of each data point and visualized the longitudinal and latitudinal movements associated with each day. A consistent longitudinal movement (e.g. ~5 consecutive data points with longitudinal shift $\geq 5^\circ\text{E}$) was considered to be a directional movement. For each individual, we defined the non-breeding period as the period comprising the date of departure from the breeding colony to the non-breeding grounds and the date they returned on land at Kerguelen Island for the subsequent breeding season. The return date on land at Kerguelen Island was determined when the GLS was dry for more than 8 hr, indicating that the bird was on land, since albatrosses do not fly for longer amount of time when foraging around Kerguelen Island (H. Weimerskirch, unpublished data). Migratory dates were considered as the number of days since the 1 January in the statistical analyses.

We conducted kernel analysis to map the density distribution of each bird during each month of the non-breeding period. This approach is recognized to be a useful tool to highlight important areas used by seabirds (Tancell, Phillips, Xavier, Tarling, & Sutherland, 2013). Kernels were calculated using the kernelUD function in the “adehabitatHR” package (Calenge, 2006). Based on our GLS data, the non-breeding period was decomposed into two distinct periods: the wintering period, from the departure date from the breeding colony to the return date to the Kerguelen sector defined by the longitude 75°E and 60°E, and the pre-breeding period, from the arrival date to the Kerguelen sector to the return date on land at Kerguelen Island (Figure 1). During the wintering period, albatrosses successively visited two geographically distinct sectors off Australia, between April and June for the first sector, and between July and September for the second sector (Figure 1). Birds that left the breeding colony and reached the wintering grounds before April were only individuals that failed to fledge a chick. Therefore, we only considered activity data after April so that birds of different breeding status had comparable tracking durations.

In addition to light levels, Mk4, Mk5, Mk9, Mk15 and Mk3006 GLS tested for saltwater immersion every 3 s and recorded the number of positive tests every 10 min, and Mk19 loggers recorded the actual duration of immersion in saltwater. Saltwater immersion data allowed estimating two activity variables: (1) the percentage of daily time spent sitting on the water and (2) the minimal number of daily transitions between air and water summed over all 10-min

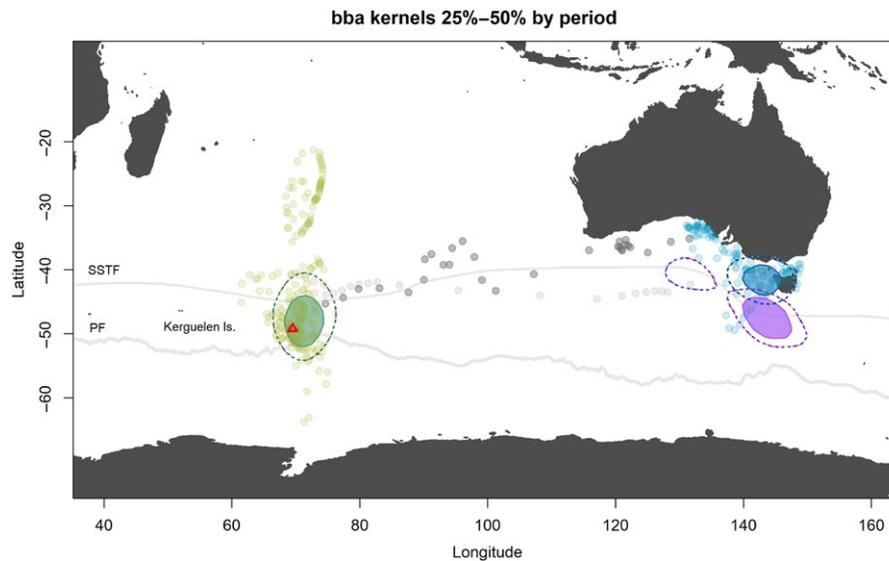


FIGURE 1 Density distribution of the Kerguelen Island population of black-browed albatross during the pre-breeding and breeding periods (in green) and the wintering periods (in blue for winter sector 1 and in purple for the winter sector 2). Areas delimited by a dotted line represent the 50% kernels for all birds. The coloured areas represent the 25% kernels of the birds. Locations of an individual typical track are illustrated with dots. Locations during the outward migration are represented by dark grey dots while locations during the inward migration are represented by light grey dots. The location of Kerguelen Island is represented by a red triangle

periods so that data from the two types of loggers are comparable. This latter measure is considered to be a good proxy of energy expenditure in albatrosses, higher number of landing and take-off resulting in increased energy expenditure (Shaffer, Costa, & Weimerskirch, 2003). As the black-browed albatross is a diurnal species and that most foraging activity takes place during daylight (Mackley et al., 2010), we focused our study on the data collected during daylight only.

Global location sensor also recorded the SST when the logger was immersed in water (sensor range: -20°C to 60°C , accuracy $\pm 0.5^{\circ}\text{C}$). SST data and activity data (i.e. proportion of time spent on the water and number of transitions air/water) were averaged by individual, years and wintering sectors (wintering sectors 1, 2 and pre-breeding sector). Some GLS failed to record SST. Incomplete datasets were still included in the analyses that did not test for an effect of SST on activity and breeding parameters. Therefore, sample sizes varied slightly between models testing different dependent variables (from 64 to 86 birds and 118 to 146 trips, see Appendix S1 for full details).

2.3 | Statistical analyses

Two sets of analyses were conducted. First, we investigated how SST and individual factors (sex, reproductive status) affected the foraging behaviour of black-browed albatrosses during the non-breeding season and their spring migration. We modelled the effects of SST (linear and quadratic effects to test for optimal type responses), sex and previous reproductive status, included as predictors, on the activity variables (proportion of time spent on the water and number of transition air/water in wintering sectors 1 and 2 and in the pre-breeding grounds), the duration of the wintering and pre-breeding

periods and the return dates to the pre-breeding grounds and land, which were the response variables.

Models including interactions between all predictor variables (i.e. SST, sex and reproductive status) were not tested because of the limited data points; however, interaction between reproductive status and sex was considered. We used generalized linear mixed models (GLMMs) fitted with a Poisson distribution (log link function) for modelling the duration of the wintering and pre-breeding periods and the return dates to the pre-breeding grounds and land. We used linear mixed models to model the number of transitions air/water and the proportion of time spent on water. Whenever the interaction term between reproductive status and sex was retained in the best model, separate models were run for each sex.

Second, we investigated the effects of the activity variables, the duration of the wintering and pre-breeding periods and the return dates in the Kerguelen sector and on land (predictor variables) on the reproductive success (response variable) in two models: one for wintering and one for pre-breeding. We used GLMMs fitted with a binomial distribution (logit link function).

Random effects of year and individual were included in the models to account for interannual variation and multiple measures on the same individual, respectively. We built candidate models from all possible combinations of predictor variables and compared candidate models based on Akaike's information criterion (AIC) and selected the model structure that minimized AIC (Burnham & Anderson, 2002). When ΔAIC between models was < 2 (i.e. the models were equally good at describing the data), we chose the most parsimonious model with the lowest number of parameters. In the case of several models with the same number of parameters, we calculated the relative variable importance by calculating the sum of Akaike weights of all models featuring a particular variable and comparing among variable

(Burnham & Anderson, 2002) and retained the model including the most relative important variables. Models were initially fitted with maximum likelihood for model selection but final models were fitted with restricted maximum likelihood to get more accurate estimates. All variables were standardized (i.e. subtract by mean and divide by standard deviation) to facilitate model fitting. Variance inflation factors of independent variables were <3 indicating no significant bias due to correlation between variables (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Analyses were carried out using R version 3.2.2 (R Core Team, 2015). All means are given \pm standard error, unless otherwise specified.

3 | RESULTS

3.1 | Intrinsic effects on foraging behaviour and timing of migration

The amount of time spent in the wintering grounds by adult black-browed albatrosses depended on the birds' previous breeding status (Table 1, Appendix S2—Table S2.3a and b). Specifically, individuals that failed to fledge a chick during the previous breeding season (i.e. failed breeders) spent significantly more time in the wintering grounds than successful breeders (Figure 2, Appendix S2—Table S2.3a and b). In addition, for a given breeding state, the wintering

period was longer for females than for males (Figure 2, Appendix S2—Table S2.3a and b).

Concerning at-sea activity, in both wintering sectors, failed breeders tended to make more take-offs and landings than successful breeders (Table 1, Figure 3, Appendix S2—Table S2.1a and b). We also detected a difference between sexes in the second but not the first wintering sector (Table 1, Appendix S2—Table S2.1a and b); in the second sector, females of a given breeding status tended to make more take-offs and landings than males of the same breeding status (Figure 3). However, neither the breeding status nor the sex had an influence on the proportion of time birds spent on the water in the wintering grounds (Table 1, Appendix S2—Table S2.2a and b).

The most parsimonious model explaining the variation in the return date to the pre-breeding grounds retained the previous breeding status and sex as explanatory variables (Table 1, Appendix S2—Table S2.4a and b). Previously failed males were the earliest to return to the pre-breeding grounds while previously successful females were the latest (Figure 4).

The duration of the pre-breeding period also varied according to the sex and the previous breeding status (Table 1, Appendix S2—Table S2.5a and b). In both sexes, individuals that successfully fledged a chick during the previous breeding season had a shorter pre-breeding period the following season, compared to

Response variable	Predictor variable		
	Sex	Breeding status	Sea surface temperature
Transition air/water (winter sector 1)		(.04)	
Transition air/water (winter sector 2)	(.002)	(.008)	
Transition air/water (pre-breeding)			
Time on water (winter sector 1)			
Time on water (winter sector 2)			
Time on water (pre-breeding)			
Return date on pre-breeding grounds	(.034)	(<.001)	- winter sector 2 (.044)
Return date on land	(<.001)		
Winter duration	(.001)	(<.001)	
Pre-breeding duration females	NA	(<.001)	
Pre-breeding duration males	NA	(<.001)	+/- pre-breeding grounds (linear <.001, quadratic <.001)

TABLE 1 Summary of the effects of sex, previous breeding status and sea surface temperature on foraging activity and timing of migration of black-browed albatrosses at Cañon des Sourcils Noirs, Kerguelen

Values in parentheses indicate *p*-values obtained from the selected models. - and +/- indicate linear negative and quadratic relationships, respectively. The interaction term between reproductive status and sex was retained in the most parsimonious model explaining the duration of the pre-breeding period (Appendix S2—Table S2.5a and b). Separate models were therefore run for each sex. Only significant results are shown.

failed breeders ($25.23 \text{ days} \pm 0.15$ for previously failed females vs. $16.81 \text{ days} \pm 0.09$ for previously successful females, see Figure 5 for males).

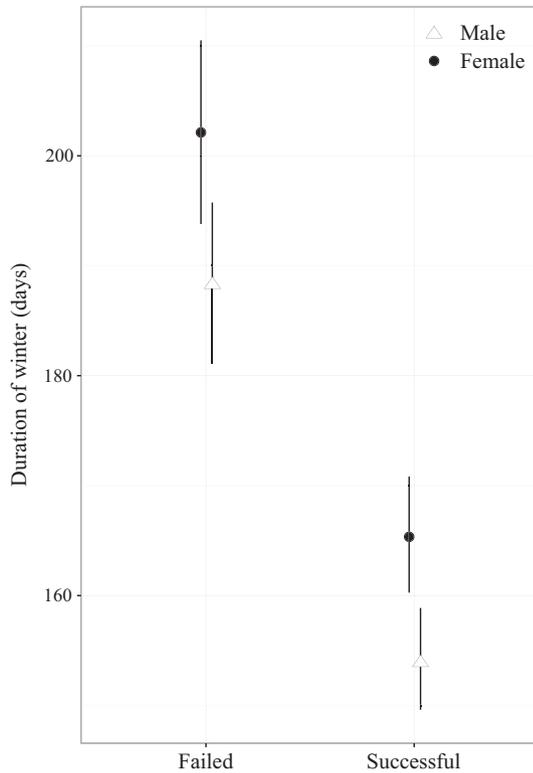


FIGURE 2 Predicted duration of winter ($\pm SE$) by reproductive state in the previous breeding season and sex in the black-browed albatross population of Kerguelen Island. Filled dots and open triangles represent females and males, respectively. Estimates were obtained from the most parsimonious model (see Appendix S2)

Finally, the return date on land at Kerguelen Island was influenced by the sex (Table 1, Appendix S2–Table S2.6a and b) with male returning earlier (3 October, 95% CI: 29 September–7 October) to the breeding colony than females (18 October, 95% CI: 13 October–22 October).

3.2 | Links between SST, foraging behaviour and migratory schedules

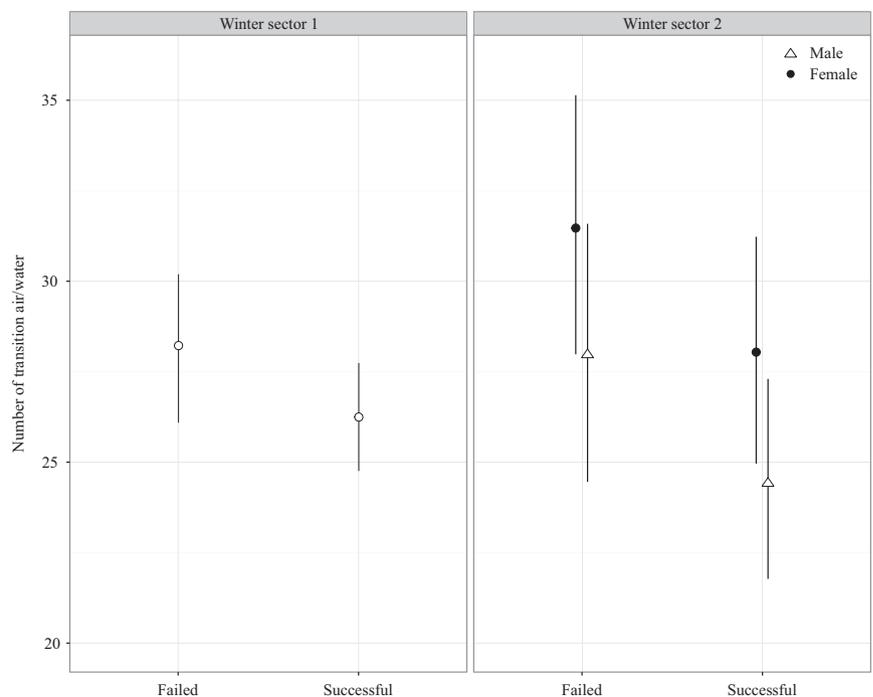
We did not detect any effect of SST on the wintering duration (Table 1, Appendix S2–Table S2.3a) and on the proportion of time birds spent on the water in the wintering grounds (Table 1, Appendix S2–Table S2.2a). SST in wintering sector 2, but not in wintering sector 1, affected the return date to the pre-breeding grounds (Table 1, Appendix S2–Table S2.4a and b): lower SST in the second wintering sector resulted in delayed return dates to the pre-breeding grounds.

The most parsimonious model retained the SST in its quadratic form as an explanatory variable for the pre-breeding period duration in male but not female black-browed albatrosses (Table 1, Appendix S2–Table S2.5a and b): at low and high SST, the pre-breeding period was shorter than at moderate SST (Figure 5). SST did not appear to explain the at-sea activities of birds during the pre-breeding period (Table 1, Appendix S2–Table S2.1a and S2.2a) and their return date on land (Table 1, Appendix S2–Table S2.6a).

3.3 | Influence of foraging behaviour and timing of migration on reproductive success

Estimation of the relative importance of explanatory variables indicated that several variables influenced breeding success by themselves, but the return date to the pre-breeding grounds was the

FIGURE 3 Number of landings and take-offs ($\pm SE$) by wintering sector, reproductive state in the previous breeding season and sex of black-browed albatross at Kerguelen Island. Filled dots and open triangles represent females and males, respectively. Open dots correspond to sex-independent estimates. Estimates were obtained from the most parsimonious model (see Appendix S2)



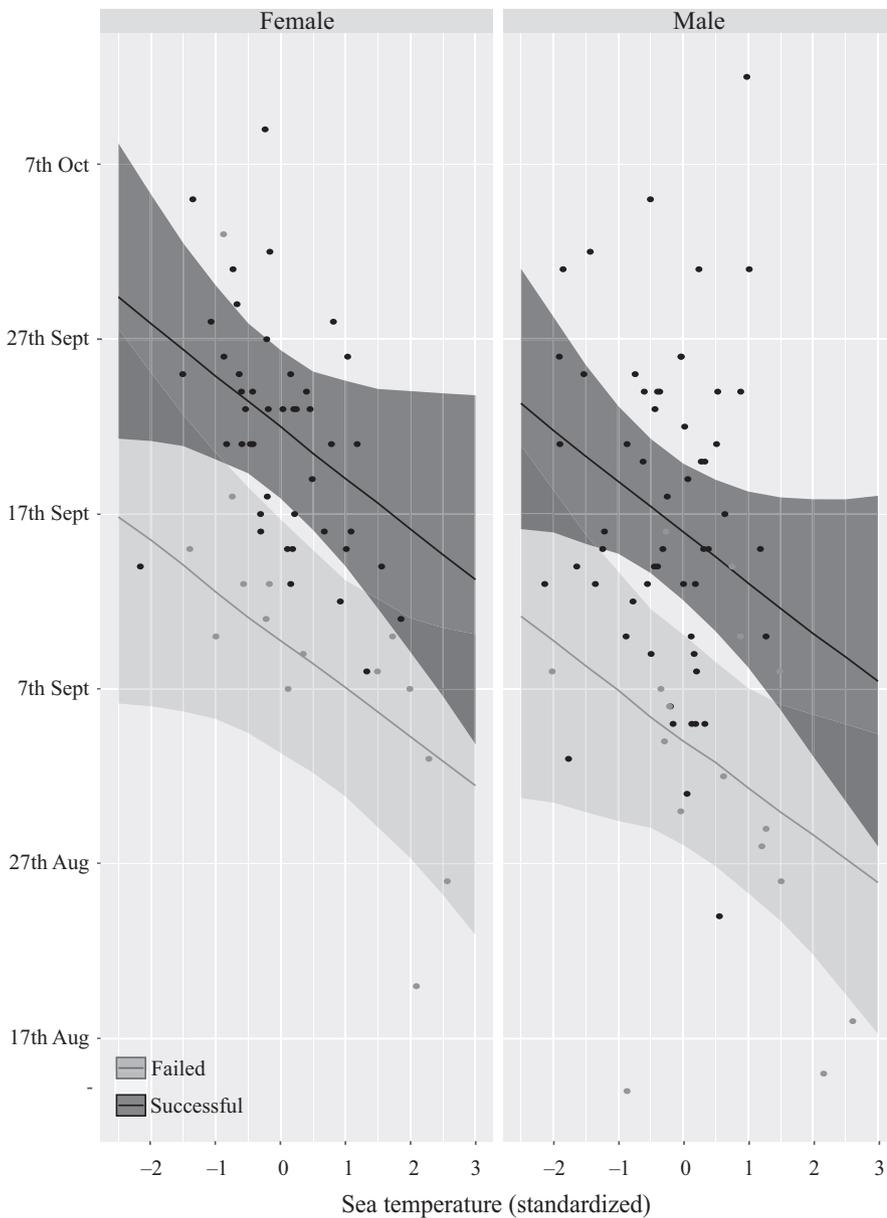


FIGURE 4 Effect of the sea surface temperature in the second wintering sector on the return date to the pre-breeding grounds in females and males black-browed albatross at Kerguelen Island. Estimates for successful and failed breeders of the previous breeding season are represented by darker and lighter grey lines, circles and shaded areas, respectively. Solid circles correspond to the observed data, while solid lines correspond to the estimates obtained from the most parsimonious model (see Appendix S2). The shaded area represents 95% confidence intervals. See Appendix S3 for a version of this figure with values of SST not standardized

variable that had the most important effect on the probability to breed successfully (weight = 0.69 vs. <0.53 for the other explanatory variables) (Appendix S2—Table S2.7a, b and c). A later return to the pre-breeding grounds was associated with a higher probability to successfully fledge a chick in the subsequent breeding season (Figure 6a).

Foraging behaviour during the beginning of the non-breeding season did not influence individual's reproductive performance. However, both the daily number of transitions air/water and the daily proportion of time spent on water during the pre-breeding period influenced the probability to breed successfully during the subsequent breeding season (Table 2, Appendix S2—Table S2.8a and b). More active birds were more likely to be successful breeders. Specifically, the probability to breed successfully increased with the number of take-offs and landings and decreased with the proportion of time spent on the water (Figure 6b and c). There

was no difference in the breeding success of tracked birds and the breeding success recorded on the wider monitored colony (Appendix S2—Table S2.9).

4 | DISCUSSION

The non-breeding period is a poorly known, yet probably critical, period of the life cycle for many migratory species. Here, we provided insights into the underlying behavioural processes through which SST in the wintering grounds, and individual characteristics, affected black-browed albatross reproductive performance. We showed that the individual reproductive performance was affected by at-sea activity during the pre-breeding season and by the return date to the pre-breeding grounds, which was affected by SST in the wintering areas.

FIGURE 5 Effect of the sea surface temperature in the Kerguelen grounds on the duration of the pre-breeding period in failed and successful male breeders of the previous breeding season for the black-browed albatross population of Kerguelen. Solid circles correspond to the observed data, while the solid lines correspond to the estimates obtained from the most parsimonious model (see Appendix S2). The shaded areas represent 95% confidence intervals. See Appendix S3 for a version of this figure with values of SST not standardized

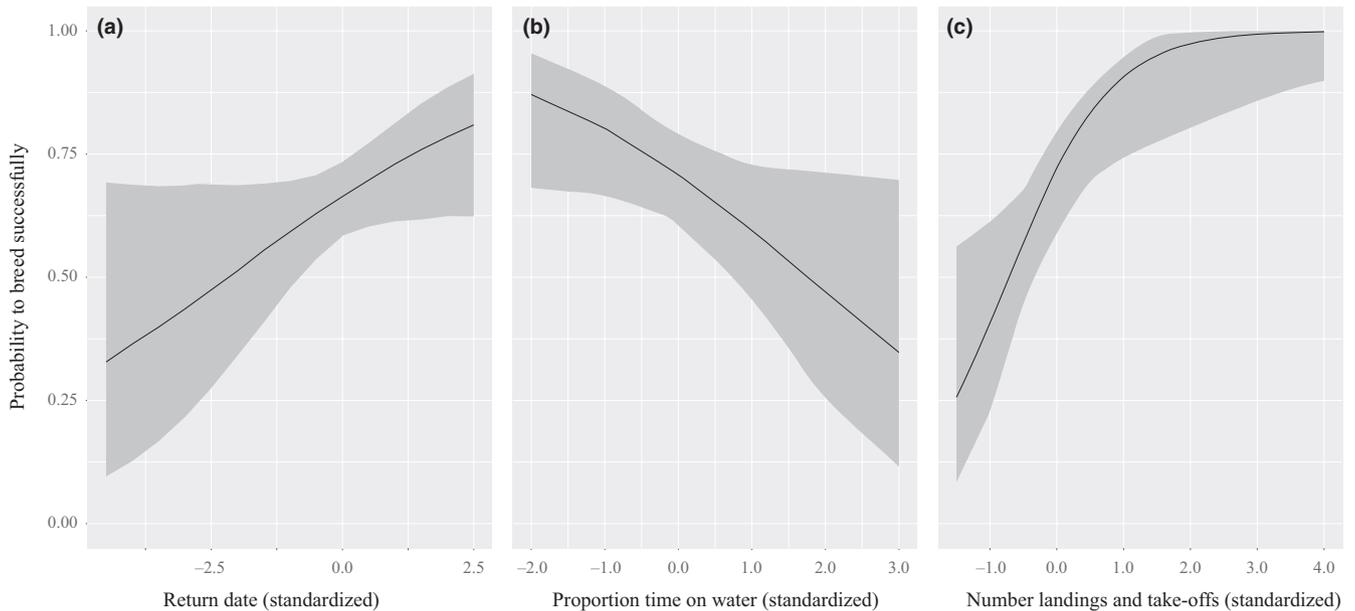
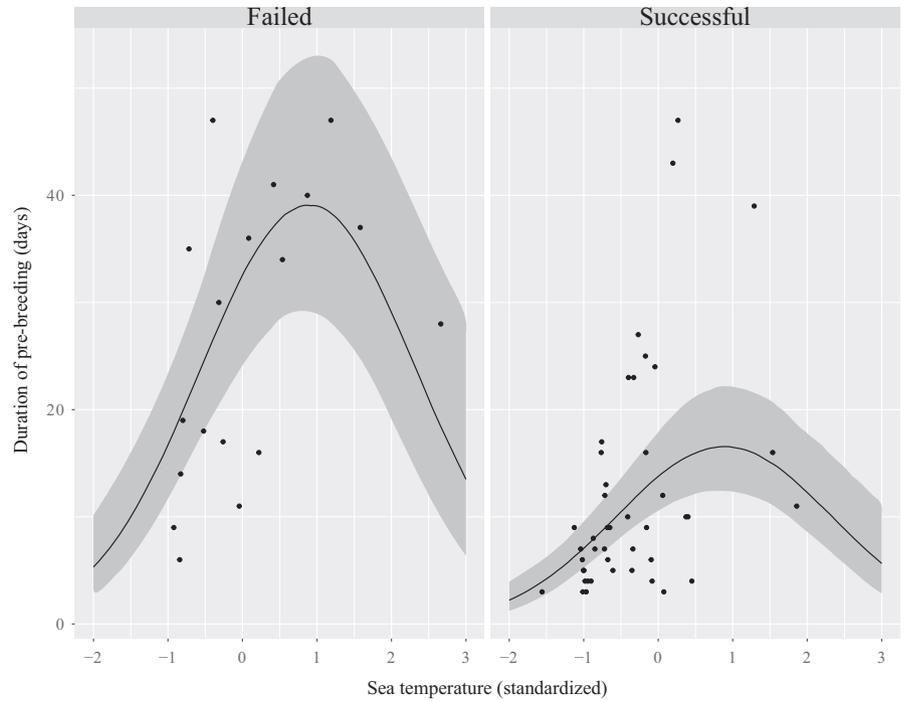


FIGURE 6 Probability to breed successfully in the black-browed albatross from Kerguelen Island according to (a) the return date to the pre-breeding grounds (in number of days since the first January), (b) the proportion of time spent on water in the pre-breeding grounds and (c) the number of landings and take-offs done in the pre-breeding grounds. The solid lines correspond to the estimates obtained from the most parsimonious models (see Appendix S2). The shaded areas represent 95% confidence intervals. See Appendix S3 for a version of this figure with no standardized values

4.1 | Impact of intrinsic factors on foraging behaviour during non-breeding period

Foraging behaviour of black-browed albatrosses during the non-breeding season varied according to the individual reproductive state. Birds that failed to fledge a chick left the breeding colony to the wintering grounds earlier than birds that successfully fledged

a chick. This pattern has been documented in other black-bowed albatross populations (Phillips et al., 2005) and other species such as black-legged kittiwakes *Rissa tridactyla* (Bogdanova et al., 2011), savanna sparrows *Passerculus sandwichensis* (Mitchell, Newman, Wikelski, & Ryan Norris, 2012), Cory's shearwaters *Calonectris diomedea* (Catry, Dias, Phillips, & Granadeiro, 2013) and grey-headed albatrosses *Thalassarche chrysostoma* (Clay et al., 2016). Consequently,

TABLE 2 Summary of the effects of foraging activity and timing of migration on breeding success of black-browed albatrosses at Cañon des Sourcils Noirs, Kerguelen

Predictor variable	Breeding success
Transition air/water wintering sector 1	
Transition air/water wintering sector 2	
Transition air/water (pre-breeding)	+ (.009)
Time on water wintering sector 1	
Time on water wintering sector 2	
Time on water pre-breeding	- (.04)
Return date on pre-breeding grounds	+ (.08)
Return date on land	
Winter duration	
Pre-breeding duration	

Values in parentheses indicate *p*-values obtained from the selected models. – and + indicate linear negative and linear positive relationships, respectively. Only significant results are shown.

failed breeders had a longer wintering period than successful breeders despite an earlier return to the pre-breeding grounds. Such an early return and extended winter and pre-breeding periods might reflect the fact that failed breeders require longer foraging periods to build the energetic reserves necessary to reproduce compared to successful breeders, indicating a lower intrinsic quality of these individuals (*sensu* Wilson & Nussey, 2010).

This hypothesis was further supported by the fact that failed breeders tended to conduct more take-offs and landings during the winter, suggesting a higher foraging effort, than previously successful breeders. Failed breeders may therefore increase their foraging activity during winter to try to compensate for their own poor condition. Difference in foraging activity between birds of different reproductive status is thought to reflect different foraging performances as a result from differences in age, experience and/or individual quality (e.g. below average resource acquisition abilities) and/or different energetic requirements (Phillips, Lewis, González-Solís, & Daunt, 2017). Previous studies have reported that birds having a higher foraging activity during winter were more likely to fail to reproduce during the subsequent breeding season (Daunt et al., 2014; Kazama et al., 2013; Shoji et al., 2015). Individuals seemed therefore to adapt their winter foraging effort as a constrained response to their own body condition rather than as an active decision concerning future breeding (Fayet et al., 2016; Shoji et al., 2015).

The foraging behaviour during the non-breeding season also differed between sexes. To our knowledge, only one study reported different at-sea foraging activity between sexes in a migratory seabird species (Fayet, Shoji, Freeman, Perrins, & Guilford, 2017). We found that females tended to have higher foraging activity (i.e. more take-offs and landings) in late winter, a longer wintering period and later return dates to the pre-breeding grounds and Kerguelen Island than males. Protandry, the early timing of life-history events in males, is common in many taxa in which individuals of the two sexes migrate to the breeding site (Morbey & Ydenberg, 2001). In

migratory birds, three non-mutually exclusive hypotheses have been proposed to explain the evolution of protandry (Morbey & Ydenberg, 2001): the “mate advantage” hypothesis that predicts early-arriving individuals may gain a fitness increase through extra-pair matings (Scott, 1977), the “rank advantage” hypothesis that assumes that early arrival leads to the occupation of high-quality territories, the territorial sex arriving earlier than the other sex (Ketterson & Nolan, 1976) and the “susceptibility” hypothesis that proposes that protandry should evolve when environmental conditions at arrival on the breeding grounds differentially affect males and females, with male being better able to cope with conditions early in the breeding season (Ketterson & Nolan, 1983). Black-browed albatrosses are territorial during the nesting period and males are presumed to return earlier to the breeding colonies than females as they have a greater role in nest acquisition and defence (Phillips et al., 2005), therefore supporting the “rank advantage” hypothesis. However, the “susceptibility hypothesis” may also be a strong force behind the evolution of protandry because females have to bear the energetic cost of the egg production and are thus likely to be more susceptible to adverse environmental conditions in the pre-breeding grounds than males. Crossin et al. (2012) showed that a female decision to breed or not, and therefore to devote resources towards egg production or not, was strongly associated with post-migratory body condition.

Females may therefore spend more time in the wintering grounds and increase their foraging activity prior to their departure in prevision to this post-migratory energetic cost. In the light of our results, we suggest that the existence of different energetic constraints and requirements between sexes may play a crucial role in determining the intersexual differences in the timing of arrival at the breeding grounds in migratory populations.

4.2 | Effect of SST on foraging behaviour during the non-breeding season

Black-browed albatrosses appeared to respond primarily to changes in climate conditions by modifying their migratory schedules rather than by modifying their at-sea activity pattern. This is particularly interesting as long-distant migratory species are often claimed to be limited in their individual plasticity in migration timing because of a rigid endogenous control of migration schedules and an inability to predict environmental conditions at their distant breeding grounds (Both & Visser, 2001; Knudsen et al., 2011). Yet, our study strongly suggests that long-distant migrants have the abilities to adjust their migration schedules to winter environmental conditions (Cotton, 2003; van Bemmelen et al., 2017).

Advancement of the spring migration when environmental conditions in the wintering grounds are more favourable has been reported in passerines and waders (Gunnarsson et al., 2006; Hüppop & Hüppop, 2003; Knudsen et al., 2011; Marra, Hobson, & Holmes, 1998; Saino et al., 2004). However, our results suggest the opposite pattern in the black-browed albatross as they tended to advance their spring migration when environmental conditions during winter were assumed to be unfavourable. Indeed, an earlier return date to

the pre-breeding grounds was associated with higher SST in the second wintering sector. Warm SST is known to have a negative effect on primary and secondary production in several marine ecosystems (Behrenfeld et al., 2006; Wilson & Adamec, 2002) and have been negatively linked to various demographic traits in several species of seabirds (Barbraud et al., 2012). In particular, in this population of black-browed albatross, Rolland et al. (2008) reported a negative correlation between high SST in Tasmanian waters (i.e. wintering foraging grounds) and the subsequent breeding success. High SST was assumed to reflect the effects of limited food resources. Therefore, black-browed albatrosses may try to minimize the energetic expenditure relative to their prey intake by leaving their wintering grounds earlier when SST was higher. Interestingly, an early return date to the pre-breeding grounds was also associated with a longer subsequent pre-breeding period suggesting that birds tried to compensate poor conditions in wintering grounds by leaving earlier and extending their foraging time in the Kerguelen sector prior to the beginning of the reproduction.

For males, the duration of the pre-breeding period followed a quadratic relationship with temperature such that moderate temperatures were associated with long pre-breeding periods. This relationship was paradoxical as we did not detect an influence of the temperature on the return date on land, which is strongly linked to the length of the pre-breeding period.

Several potential biases may explain the quadratic relationship we detected. First, the temperature values were averaged over the pre-breeding period but the length of this period varied widely between individuals. Therefore, the range of values recorded for males with short pre-breeding periods was likely much less important than the range recorded for birds with longer pre-breeding periods. This may lead to the calculation of warmer/colder mean temperatures in males with short pre-breeding period and to more moderate values in males with longer pre-breeding periods. Another potential bias may result from the fact that male albatrosses visit different areas of the pre-breeding grounds and use different water masses (from sub-Antarctic to subtropical waters) depending on the date they return to the pre-breeding grounds. Unfortunately, the spatial resolution of the GLS was too low to allow us to verify such hypothesis.

4.3 | Impact of foraging behaviour during the non-breeding season on breeding success

The breeding success of black-browed albatrosses was influenced by the time they returned to the pre-breeding grounds and by their foraging activity during the pre-breeding period. Specifically, an early return to the pre-breeding grounds and a low foraging activity during the pre-breeding period were associated with a lower probability to breed successfully.

4.3.1 | Spring migratory schedules

The return date to the pre-breeding grounds depended on both environmental and individual factors. Individuals returned earlier to

the pre-breeding grounds and therefore had a lower probability to breed successfully, when environmental conditions in the wintering grounds (sector 2) were unfavourable (i.e. high SST). The existence of carry-over effect of winter conditions on demographic parameters has been reported in several species of migratory birds (Alves et al., 2013; Bogdanova et al., 2017; Daunt et al., 2014; Frederiksen, Daunt, Harris, & Wanless, 2008; Guéry et al., 2017; Nevoux et al., 2007; Rolland et al., 2008) and climate-induced changes in the food webs and/or foraging behaviour were often suggested to explain such effect. Nonetheless, our study is one of the first to investigate the behavioural mechanisms underlying the linkage between climatic conditions during winter and subsequent reproductive performance in a long-distant migrant bird (but see Bogdanova et al., 2011, 2017).

Flexibility in migratory behaviour has been recognized to be a critical feature to adapt to climate change (Møller et al., 2008; Pulido, 2007). However, an earlier return to the pre-breeding grounds was not enough to buffer black-browed albatross' reproductive success against poor winter conditions, since an earlier return was linked to lower breeding success. Alternatively, spring migratory schedules of black-browed albatross may depend on environmental cues that are no longer reliable under some climatic conditions associated with high SST.

Our results indicate that previously failed breeders tended to return earlier to the pre-breeding grounds and therefore had a higher risk to fail the subsequent reproduction, than previously successful breeders. Negative covariation among life-history traits is common in studies of long-lived species (e.g. failure to breed in year t is associated with lower chances of surviving and breeding successfully in $t + 1$ [Cam, Link, Cooch, Monnat, & Danchin, 2002; Aubry, Koons, Monnat, & Cam, 2009]) and are generally considered to reflect heterogeneity in individuals ability to acquire resources (Van Noordwijk & de Jong, 1986). In agreement with this hypothesis, failed and successful breeders had different foraging behaviour but, despite increasing their winter foraging activity and extending their wintering and pre-breeding periods, failed breeders were still associated to a higher risk of a subsequent breeding failure likely reflecting a persistent individual difference in reproductive status (Jenouvrier et al., 2015).

Finally, there was no effect of the return date on land on breeding success. Return date on land, as determined here, may not be a good proxy for the return date at the colony, since a bird may have returned on land for a few hours and may have gone back at sea afterwards.

4.3.2 | At-sea foraging activity

During the pre-breeding period, birds that spent more time in flight and conducted more take-offs and landings (i.e. likely having a higher foraging effort) were more likely to breed successfully during the subsequent breeding season. This activity pattern strongly suggests that more active individuals were able to accumulate more energetic reserves in prevision of the breeding season and were therefore better able to cope with the high energetic demands

associated with reproduction. This result contrasts with our previous suggestion that increased foraging activity during winter was used to compensate individuals' poor condition, but concur with some studies that found evidence that pre-breeding diet quality influences subsequent reproductive success in Cassin's auklets *Ptychoramphus aleuticus* (Sorensen, Hipfner, Kyser, & Norris, 2009). This change in the foraging activity pattern across seasons for the black-browed albatross may reflect different constraints across the life cycle, and several studies on migrant seabirds have reported a similar change between winter and breeding seasons (Delord et al., 2016; Mackley et al., 2010, 2011). During the winter, central place foragers such as albatrosses do not have to cope with the reproductive costs and the central place constraint. Therefore, they are able to minimize their energetic costs to self-maintenance and to keep their foraging activity at the lowest. At-sea activity is also strongly constrained by moulting (Cherel, Quillfeldt, Delord, & Weimerskirch, 2016; Weimerskirch, 1991). During the pre-breeding and breeding periods, energetic demands increase requiring a more intense foraging effort. Consequently, an intense foraging activity may reflect the "poor" condition of individuals or differences in moulting during the winter when energetic costs are supposedly at their minimum, while it may reflect the higher energetic requirements faced by individuals during the pre-breeding and breeding periods. This result highlights the fact that some periods of the non-breeding season may be more critical than others in terms of energetic requirements and impact on the subsequent individual reproductive success.

5 | CONCLUSION

Our study provided a unique insight into the behavioural mechanisms underlying the linkage between climatic winter conditions and reproductive performance in a long-distant migrant seabird. We demonstrated the existence of carry-over effects of the late winter environmental conditions and pre-breeding foraging activity on the reproductive performance of the black-browed albatross. By contrast, the climatic conditions and foraging behaviour during the beginning of the non-breeding season did not influence individual's reproductive performance highlighting the differential impact of the non-breeding periods on life-history traits. Exploring climate effects on the foraging behaviour during the full life cycle and its effects on demographic parameters is therefore essential to predict more accurately how environmental change may influence population dynamics.

Interestingly, black-browed albatrosses responded to late winter climatic conditions by adapting their migratory schedules rather than modifying their foraging activity. Foraging activity may be constrained at this stage, and birds can only adjust the timing of migration. A recent demographic study (Jenouvrier et al., 2018) shows that changes in late winter climatic conditions affecting their migratory schedules have little impact on the population growth rate. However, the direct effects of adult foraging activity during pre-breeding on breeding success have a larger influence

on the population growth rate. SST of the Southern Ocean is expected to increase in the future (Collins et al., 2013) but a population of individuals with the optimal foraging activity could buffer the negative impact of unfavourable climate conditions, at least on the short-term. Future studies should consider migratory and foraging behaviours during the non-breeding season as important determinants of the variation in subsequent individual fitness and population dynamics.

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AUTHORS' CONTRIBUTIONS

H.W., C.B. and S.J. conceived the ideas; C.B. and H.W. obtained the funding for fieldwork and designed methodology for the GLS deployment and analysis; C.B., H.W. and K.D. collected the data; K.D. managed the demographic database, managed and analysed the GLS data; S.J. obtained the funding for the demographic analyses; M.D., S.J. and C.B. designed statistical methodology; M.D. performed the statistical analysis; M.D. wrote the first draft of the manuscript; all authors contributed to the draft of the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.pb209db> (Desprez, Jenouvrier, Barbraud, Delord, & Weimerskirch, 2018).

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