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Author for correspondence:
Francesco Ventura
e-mail: fraventura.92@gmail.com

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Environmental variability directly affects the prevalence of divorce in monogamous albatrosses

Francesco Ventura[1], José Pedro Granadeiro[1], Paul M. Lukacs[2], Amanda Kuepfer[3,4] and Paulo Catry[5]

[1]CESAM, Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, Lisboa 1749-016, Portugal
[2]Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W. A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA
[3]SAERI—South Atlantic Environmental Research Institute, Stanley, Falkland Islands FIQQ 1ZZ, UK
[4]Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn TR10 9FE, UK
[5]MARE – Marine and Environmental Sciences Centre, ISPA – Instituto Universitário, Rua Jardim do Tabaco 34, Lisboa 1149-041, Portugal

FV, 0000-0002-1584-2433; JPG, 0000-0002-7207-3474; AK, 0000-0002-3559-8802

In many socially monogamous species, divorce is a strategy used to correct for sub-optimal partnerships and is informed by measures of previous breeding performance. The environment affects the productivity and survival of populations, thus indirectly affecting divorce via changes in demographic rates. However, whether environmental fluctuations directly modulate the prevalence of divorce in a population remains poorly understood. Here, using a longitudinal dataset on the long-lived black-browed albatross (*Thalassarche melanophris*) as a model organism, we test the hypothesis that environmental variability directly affects divorce. We found that divorce rate varied across years (1% to 8%). Individuals were more likely to divorce after breeding failures. However, regardless of previous breeding performance, the probability of divorce was directly affected by the environment, increasing in years with warm sea surface temperature anomalies (SSTA). Furthermore, our state-space models show that warm SSTA increased the probability of switching mates in females in successful relationships. For the first time, to our knowledge, we document the disruptive effects of challenging environmental conditions on the breeding processes of a monogamous population, potentially mediated by higher reproductive costs, changes in phenology and physiological stress. Environmentally driven divorce may therefore represent an overlooked consequence of global change.

1. Background

Social monogamy is a widespread mating system, almost ubiquitous in birds, shared by over 90% of avian species [1] and also present in some mammal species in the orders Primates, Macroscelidea and Carnivora [2]. Different species exhibit various degrees of fidelity to their mate, resulting in different rates of maintenance of pair bonds, which is a function of the rates of widowing but also of divorce [3,4]. Owing to intra-sexual competition, the choice of mate is seldom unconstrained and many individuals in the population have to settle with a sub-optimal partnership. Across a wide range of species, divorce was found to be a strategy aimed at correcting for these sub-optimal partnerships, resulting in an improvement of the reproductive success of one or both members of the pair [4–6].

Divorce is often an adaptive behavioural mechanism driven by the ‘win–stay, lose–switch’ information gathering process, in which measures of previous breeding performance inform the decision of an individual to re-mate with their old partner (stay) or find a new one (switch) [3,7,8]. Several studies on monogamous birds (reviewed in [4]) showed that divorce is triggered by breeding failure and that, in terms of breeding success improvements, females benefitted from divorce more than males (suggesting their role as the 'choosy' sex). The strength of the relationship between failure and divorce and the variability in divorce rates among different species have been widely investigated in light of the species-specific life-history traits, which in turn determine the advantages and disadvantages of mate-change [3,9,10]. For instance, in long-lived seabirds, the benefits resulting from breeding with the same partner (improved experience and coordination between the pair members owing to mate familiarity) and the high mate survival probability (which limits the costs of waiting in vain for the reunion with the old partner), as well as the costs involved in attracting and pairing with a new mate, result in low divorce rates [3,7,11].

Environmental conditions affect the survival and productivity rates in a population; in turn, this may lead to an indirect link between the environment and divorce, mediated by changes in demographic rates. In addition to that, there is some evidence that environmental conditions and habitat characteristics might play an important direct role in affecting the rate of divorce in a population [5,12]. Some studies supported the 'habitat-mediated' hypothesis, suggesting that divorce is more common in unstable and lower quality environments [4,5,13,14]. However, this hypothesis has seldom been comprehensively tested, and in particular it has only been assessed by focussing on different species or on different populations of the same species in different sites. While this approach might allow for assessing the environmental drivers of divorce in populations facing a wide range of conditions, wild populations in different ecological settings often exhibit substantial ecological differences that might hinder the robustness of a comparative analysis. Conversely, the temporal variability of divorce exhibited by the same population in response to environmental changes has not been investigated. Yet, investigating the temporal variability of divorce rates in a single population monitored across multiple years may provide insights into the role of the environment on the mating strategies of individuals. In fact, in so doing, the role of environmental drivers on divorce can be robustly assessed while accounting for the demographic traits characterizing the study population and the same ecological setting characterizing the study site.

In addition to the habitat-mediated hypothesis, alternative environmental-driven mechanisms were proposed. For instance, previous studies hypothesized that, rather than being driven by the reproductive outcome *per se*, the decision of retaining or changing mate might be informed by the reproductive outcome relative to the environmental conditions experienced in a given year. Thus, environmental variability may affect the reliability of the 'win–stay, lose–switch' information gathered in previous years, potentially leading to a discounting of the importance of reproductive failures in bad years [6,15]. Moreover, the environment might directly influence the process of sexual selection via 'ecological cross-overs', i.e. through changes in preferences of mate characteristics as the environment changes [16].

In this study, we analyse a long-term demographic dataset of the black-browed albatross (*Thalassarche melanophris*) population in the Falkland Islands. The main objective of this study is to investigate whether, across years, divorce is affected by environmental variability. Owing to the indirect effects of the environment on divorce (mediated by changes in demographic rates, see above), and in order to detect direct environmental effects we adopted an analytical framework to simultaneously investigate the intrinsic (i.e. specific to the pairs, such as the previous reproductive outcome) and extrinsic (i.e. environmental) drivers of divorce. Specifically, we test the following hypotheses.

(Hp 1) Reproductive failure triggers divorce. Moreover, as early failures are potential indicators of mate sterility, incompatibility or poor parental abilities [4], we hypothesize that the timing of the breeding failure modulates the relationship between failure and divorce, with early failures being associated with a higher probability of divorce.

(Hp 2) The prevalence of divorce varies significantly across years as a result of environmental variability. Consistent with the habitat-mediated hypothesis, we hypothesize that divorce rate (at the population level) and the probability of divorce (at the individual level) are higher in lower quality years. In particular, as the productivity of this albatross population was found to be largely affected by sea surface temperature anomalies (hereafter 'SSTA', which was found to decrease the productivity of the population) and by wind intensity (hereafter 'WIND', which had instead a positive effect) [17], we predict that divorce is influenced by changes in SSTA and WIND. Specifically, we expect SSTA to positively affect and WIND to negatively affect the prevalence of divorce.

We carried out an individual-based analysis implementing generalized linear mixed effects models (GLMM) and Bayesian state space models (SSM), in which the intrinsic and extrinsic drivers of divorce were simultaneously assessed. More specifically, using GLMMs, we focussed on the effects of previous breeding performance (accounting for the timing of failure) and environmental variables on the probability of occurrence of a divorce event. Using SSMs, we formulated mate-change (differentiating between divorce and widowing) as a transition between the different 'states'; in so doing, this framework allowed for decomposing divorce into parameters (and their environmental drivers) determining the transitions between states of the breeding population [18].

2. Methods

(a) The study system and data collected

Since 2003, we have collected capture-mark-recapture data on black-browed albatrosses breeding on New Island, Falklands, home to approximately 15 500 pairs [19]. Every year, we recorded the encounter histories of every breeding bird nesting in five discrete study sub-colonies on New Island and recorded the identity of the ringed non-breeding birds observed inside or outside of our study patches. Each year, we ringed every new breeder recruiting into the study patches. The fate of each egg and chick was recorded on a daily basis during the incubation (beginning in early October) and brooding phases (starting the second week of December) and on a weekly basis during the post-brooding phase. Starting from the 2008 season, we collected GPS tracking data during incubation and brooding [20], which enabled us to quantify the oceanic areas most intensely used by albatrosses (electronic supplementary material). In a recent study [17], we found that this albatross population is increasing and that the sustained population growth is underpinned by high survival rates of both adults and juveniles and by high productivity rates.

The environmental covariates considered in this study were SSTA and WIND, which affect marine productivity through water mixing and nutrient supply and, in the case of WIND, shape habitat accessibility and transport cost [21]. Importantly, SSTA and WIND were found to greatly impact the breeding parameters of this albatross population [17]. Specifically, SSTA was found to have a strong negative effect on the probability of breeding and on breeding success, whereas WIND positively affected breeding success. Monthly multi-scale ultra-high resolution SSTA (expressed in °C) was downloaded from the National Oceanic and Atmospheric Administration at a spatial resolution of 0.01° (https://coastwatch.pfeg.noaa.gov). WIND ($\mathrm{m\,s^{-1}}$) was calculated from the meridional and zonal components reanalysis downloaded from the European Centre for Medium-Range Weather Forecasts ERA-5 database (https://cds.climate.copernicus.eu/cdsapp), at a temporal and spatial resolution of 6 h and 0.25°, respectively. Monthly average WIND rasters were calculated for each month in the study. The relevant spatial extent for the variable extraction was the 90% kernel utilization distribution [22] calculated based on the tracking data (electronic supplementary material). The environmental variables were averaged across a temporal window hypothesized to capture the scale at which the environment acts on mate-choice and divorce. Rather than an instantaneous trigger at a precise moment, we assumed that the decision-making process leading to divorce can happen at various times and may be informed and reinforced over time. We therefore opted for a conservative approach and selected a temporal window large enough to encompass relevant periods from which the decision was informed. This window spanned for a year, from the start of the previous breeding season (in October) to the end of the subsequent non-breeding season (in September) immediately preceding the focal breeding season. Thus, for instance, to investigate the environmental effects on the divorce rate in the 2005 season, we averaged the covariates between October 2004 and September 2005. Prior to the inclusion in the models, the explanatory variables were standardized to facilitate model convergence.

It is important to highlight the resolution mismatch between our detailed individual-based dataset and the yearly environmental covariates, which simultaneously affect all study individuals in a given year. As it is often the case for models deployed on longitudinal data, the analytical depth attained adopting an individual-based framework comes at the cost of exposing the analysis to the issue of pseudoreplication. In our case, this involves the association of the same value of SSTA and WIND to all birds in any given year. However, while we acknowledge that the precision of the parameters of the individual-based models might be misleadingly overestimated, our results are supported by a coarser quasi-binomial generalized linear model (GLM) quantifying the environmental effects on the yearly divorce rate (see below), in which the population-level focus is not affected by pseudoreplication.

(b) Inter-annual variability and environmental drivers of divorce rate

Consistent with the literature, a divorce event was recorded when at least one member of a breeding pair re-paired with a different mate in the following season, while the prior partner was still alive [3]. We calculated the yearly divorce rate for all study years. We used a quasi-binomial GLM to model the population divorce rate as a function of SSTA and WIND. The significance of each candidate covariates was assessed by fitting nested models in which each explanatory variable was removed in turn and the difference in scaled deviance between the full model and the model without the covariate was compared using a χ^2 test [23].

(c) Probability of divorce, timing of failure and environmental effects

To investigate the variables affecting the probability of divorce, we considered the encounter histories of all non-widowed females. To restrict our analysis exclusively on the occurrence of divorce events, the females that suffered mate loss were excluded; this resulted in a dataset comprising 2899 breeding attempts recorded for 424 females between the 2004 and the 2019 seasons. Every year, the individuals could either: remain faithful and mate with their previous partner (coded as '0'); skip a breeding attempt while their mate also did not attempt breeding (also coded as '0'); divorce and breed with a new mate (coded as '1'); or skip a breeding attempt while their previous partner bred with another mate (also considered as a divorce and thus coded as '1'). Using binomial GLMMs, we modelled the occurrence of divorce as a function of the following explanatory variables: the individual previous year breeding score; SSTA and WIND. The individual breeding score (which was preferred to breeding success because it is non-dichotomized [4]) was calculated as a categorical variable in which successfully fledging a chick was coded as '2'; failed after hatching was coded as '1'; failed before hatching was coded as '0'. Each individual identity was included as a random effect. Starting from a full model with all explanatory variables and interactions, we performed backwards model selection and removed covariates based on Akaike information criteria [24]. For completeness, the same analysis was carried out on the encounter histories of males (electronic supplementary material).

(d) Retaining mate, switching mate and environmental effects

The focus of our analysis then moved from modelling the probability of occurrence of a divorce event (described in §2c) to a finer scale, individual based investigation of mate-change (i.e. focussing on both divorce and widowing). Mate-change (owing to divorce or widowing) was formulated as transition determined by two key parameters: the probability of retaining the previous mate; and the probability of breeding after mate-change (i.e. 'switching mate' after divorce or mate loss). The objective of the analysis was to compare these parameters among previously successful, failed, non-breeding and widowed birds; and to investigate whether changes in environmental covariates affected the probability of retaining the previous mate for the different states of the breeding population. Separately for females and males, we built stage-structured Bayesian SSMs adopting a multi-event framework (figure 1; electronic supplementary material) to quantify the state-specific probabilities of retaining the previous mate ($\mathrm{breed_{STAY}}$) and of breeding after mate-change ($\mathrm{breed_{SWITCH}}$). In the models, each individual entered the cohort the year after recruiting (i.e. the year after their first breeding attempt). We specified different $\mathrm{breed_{STAY}}$ parameters for previously successful (i.e. successfully fledging a chick), failed and non-breeding individuals; and a different $\mathrm{breed_{SWITCH}}$ for previously successful, failed, non-breeding and widowed birds. In short (see the electronic supplementary material for a detailed description), the encounter histories of all females ($n = 463$) and males ($n = 477$) were retained in the analysis. Every season, the individuals were assigned to one of the following states: successful ($\mathrm{S_{OLD}}$) or failed ($\mathrm{F_{OLD}}$) with the old mate; successful ($\mathrm{S_{NEW}}$) or failed ($\mathrm{F_{NEW}}$) with a new mate; non-breeding (NonB), if they skipped a reproductive attempt and their partner was alive; widowed (Wid), if their previous mate died and they did not breed with a new one. Every time that an individual did not retain the previous mate and bred with a new mate, it transitioned to $\mathrm{S_{NEW}}$ or $\mathrm{F_{NEW}}$, depending on the outcome of the reproductive attempt. The individuals automatically transitioned to $\mathrm{S_{OLD}}$ or $\mathrm{F_{OLD}}$ after the third breeding attempt with the same new mate. When designing this SSM, we made the following two assumptions. First, to decide whether assigning non-nesting individuals to the NonB or Wid state, we assumed that their previous mates were dead if they were not seen during that breeding season and never sighted

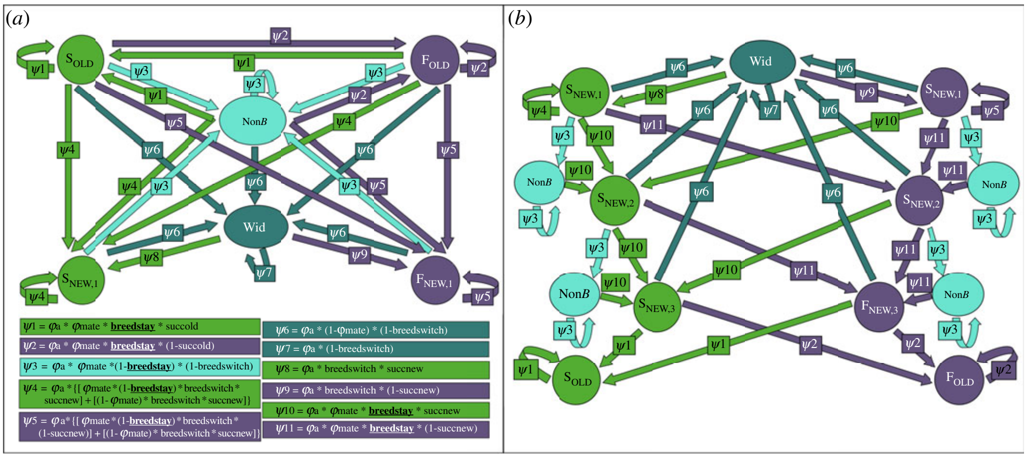

Figure 1. The multi-event stage-structured Bayesian state-space models (SSM) describing the breeding processes of the black-browed albatross population. Two separate SSMs were set up, one for females and the other for males. The models were applied to all encounter histories of females and males, including those with zero and multiple mate-changes. For clarity, the model diagram is divided in two panels. In (*a*), we represent the transitions of the 'old' states and the first year 'new' states. In (*b*), we depict the transitions of the 'new' states, which revert to 'old' after the third breeding attempt (see below and §2d in the main text). The states are: successful (S_{OLD}) or failed (F_{OLD}) birds breeding with the old mate; successful (S_{NEW}) or failed (F_{NEW}) individuals breeding with a new mate, where a relationship is defined as 'new' for the first 3 years (S/F_{new1}, S/F_{new2}, S/F_{new3}), after which the individuals automatically transition to the 'old' states; non-breeding (NonB), if they skipped breeding and their partner was alive; widowed (Wid), if their previous mate died and they did not breed with a new one. In both panels, the same names are used for the same states—i.e. NonB in (*b*) is the same state as in (*a*). The different colours are used to represent successful and failed breeders (both with an old and a new mate), non breeders and widowed. The transition probabilities between states (ψ), shown in the equation boxes at the bottom of (*a*), are driven by state-specific parameters. The complete set of state-specific parameters, determining the transitions between states, were: probability of retaining the previous mate ($breed_{STAY}$); probability of breeding after mate-change ($breed_{SWITCH}$); breeding success with the first mate ($succ_{OLD}$) or with subsequent mates ($succ_{NEW}$); individual survival (f_a); partner survival (f_{mate}). In the equation boxes, the $breed_{STAY}$ parameters for the different states are represented using bold underlined text to highlight that, within the model formulation, the environmental effects on the state-specific $breed_{STAY}$ parameters were quantified using logistic regression. (Online version in colour.)

again. The validity of this assumption is supported by the ecological features of our study population. In fact, the very high detection and survival probabilities of adult birds in our colonies (electronic supplementary material and [17]) ensure a low probability of misclassifying individuals not seen over a single sampling occasion (i.e. the probability of a bird surviving and of a failed detection), which further drops for individuals not seen over multiple seasons (see the electronic supplementary material). Furthermore, it is reasonable to expect that the occurrence of these few (if any) potential instances of erroneous state assignments would not lead to any bias regarding the relationship between the environment and divorce (electronic supplementary material). Second, we assumed that a partnership was 'new' for the first three breeding attempts, after which a mate was considered 'old'. While we acknowledge the subjectivity of this criterion, this decision was taken in order to: capture multiple mate changes; and to improve the biological realism (and therefore the parameter estimates) of the SSM by using different breeding success parameters for new pairs and for well-established, more coordinated pairs (electronic supplementary material).

Within both the female and male SSM formulations, to investigate the environmental drivers of divorce, we used univariate logistic regression to investigate the effects of SSTA and WIND on the probability of retaining the previous mate ($breed_{STAY}$). The importance of the covariates was assessed using inclusion probability parameters w [25] (electronic supplementary material).

As described above, this SSM was used to analyse the encounter histories of all individuals in our colonies, also including those that never changed mate. This was advantageous for the retrieval of unbiased '$breed_{STAY}$' and '$breed_{SWITCH}$' parameters. However, the breeding success parameters estimated in this model were not conditional on mate-change having occurred. Moreover, owing to model convergence issues, it was not possible to specify different breeding success parameters for birds that changed mate owing to divorce and owing to widowing. Therefore, separately for females and males, we designed a second SSM (electronic supplementary material) to quantify the breeding success before and after mate-change, using different parameters for birds that changed mate owing to divorce and widowing. To ensure that the estimated breeding success rates were conditional on mate-change having occurred and in order to simplify the model formulation and reach model convergence, we retained in the analysis only those individuals that changed mate once owing to widowing or divorce.

(e) State space model implementation

The SSM analysis was performed in the JAGS software executed through R [26] via the R2JAGS package [27]. The Markov chain Monte Carlo algorithm was used to sample from the posterior distribution of each SSM parameter. For all models, we generated three chains of at least 30 000 iterations. We ensured that the chains were well mixed and that the Gelman–Rubin diagnostic convergence statistic [28] was below 1.02 for all parameters.

3. Results

(a) Inter-annual variability and environmental drivers of divorce rate

The divorce rate showed a pronounced inter-annual variability (figure 2*a*): the average rate was 3.7%, ranging between 0.8% and 7.7%. The yearly estimates of divorce rate were significantly positively correlated with SSTA (Pearson's correlation, $r_{14} = 0.57$, $p = 0.02$) but not correlated with the yearly number of available widowed males (Pearson's correlation, $r_{14} = 0.22$, $p = 0.41$) and females (Pearson's correlation, $r_{14} = 0.18$, $p = 0.50$). The divorce rate increased as SSTA increased (figure 2*b*); SSTA was the only covariate retained in the quasi-binomial

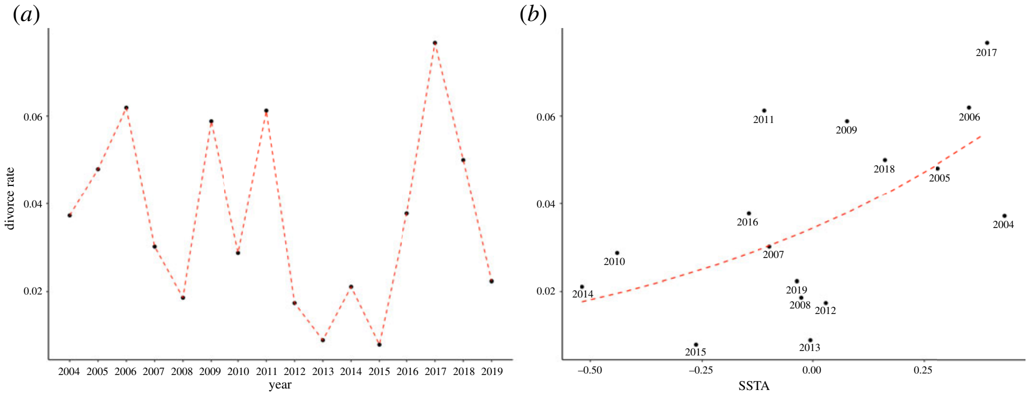

Figure 2. (*a*) The temporal variability in divorce rate between 2004 and 2019. A divorce event was recorded when at least one member of a pair re-paired with a different mate in the following season, while the old partner was still alive. (*b*) The predicted effect of sea surface temperature anomaly (SSTA) on the population divorce rate based on the quasi-binomial GLM, depicted by the dashed red line. The dots represent the observed divorce rate (on the *y*-axis) and SSTA (on the *x*-axis), with the labels specifying the year in which each observation was recorded. (Online version in colour.)

GLM ($\chi^2_1 = 6.8$, $p = 0.009$), explaining 35% of variance in divorce rate ($r^2 = 0.35$).

(b) Probability of divorce, timing of failure and environmental effects

The GLMM results show that reproductive failure, particularly at an early stage, is the main trigger of divorce. Crucially, after accounting for the effect of breeding failure, our results also show that the probability of divorce increased as SSTA increased. More specifically, the selected GLMMs retained previous breeding score and SSTA (but not their interaction) as significant predictors of the probability of divorce. Previous breeding score was the main variable affecting the probability of divorce—for females whose eggs did not hatch, divorce was approximately: 5.2 times more likely compared to females that failed after their eggs hatched; and 5.4 times more likely compared to successful birds. Additionally, consistently across the different levels of previous breeding score, the probability of occurrence of divorce increased by 1 per cent point (i.e. an increase of 0.18 on the logit scale) for an increase of one standard deviation in SSTA (electronic supplementary material). These results were largely consistent with those obtained from the analysis based on the encounter histories of males (electronic supplementary material).

(c) Retaining mate, switching mate and environmental effects

The SSM results show that: individuals that failed breeding and those that skipped a breeding attempt were less likely to retain their mate than previously successful birds; and that, after mate change, males were less likely to breed again with a new partner than females. The estimated parameters are represented in figure 3*a* (for a full description of the model results see the electronic supplementary material). In females, the probability of retaining mate (breed$_{\text{STAY}}$) was estimated at 0.97 for previously successful (95% credible interval, hereafter 'CRI': 0.95–0.98); 0.87 for failed (CRI: 0.85–0.90); and 0.11 for non-breeders (CRI: 0.07–0.16). The male estimates were in line with those for females, with the exception of non-breeding males, for which breed$_{\text{STAY}}$ was estimated at 0.08 (CRI: 0.05–0.10). In females that did not breed again with their previous mate, the probability of breeding after mate-change (breed$_{\text{SWITCH}}$) was equal to 0.45 for previously successful (CRI: 0.36–0.55); 0.47 for failed (CRI: 0.39–0.55); 0.59 for non-breeders (CRI: 0.47–0.70); and 0.85 for widowed (CRI: 0.75–0.93). In males, breed$_{\text{SWITCH}}$ was estimated at 0.26 for previously successful (CRI: 0.20–0.33); 0.26 for failed (CRI: 0.19–0.33); 0.45 for non-breeders (CRI: 0.37–0.53); and 0.65 for widowed (CRI: 0.58–0.72).

The only covariate retained in the SSMs was SSTA for previously successful females (figure 3*b*): more specifically, the probability of retaining the previous mate (breed$_{\text{STAY}}$) of previously successful females was negatively affected by SSTA (inclusion probability $w = 0.72$; $\beta_{\text{SSTA}} = -0.39$; CRI: −8.08, −8.22).

The results of the SSM formulated to quantify the breeding success before and after mate-change show that the breeding success of females improved after divorce, albeit to a marginal extent. Specifically, the female success before mate change (approx. 0.65) was lower than the breeding success after mate change in case of divorce but higher than the success attained after widowing (approx. 0.69 and approx. 0.47, respectively, see the electronic supplementary material). Conversely, in males, the breeding success estimates were only minimally different before and after mate change (approx. 0.63 before mate change; approx. 0.65 after divorce; approx. 0.66 after widowing; electronic supplementary material).

4. Discussion

A series of causal and functional explanations of divorce were proposed over the past decades, giving rise to well-established hypotheses in the ecological literature [3,4]. As we found that divorce is triggered by breeding failure and that it yields reproductive benefits (particularly so in females, which are more likely to find new partners and attain a higher breeding success), our results strongly highlight that, in a long-lived monogamous seabird population, divorce is an adaptive strategy driven by the 'win–stay, lose–switch' information gathering process. However, crucially, we also found that the divorce rate in our study population varies substantially across years and is directly modulated by temporal environmental variability, with higher divorce rates recorded in lower quality years. To the best of our

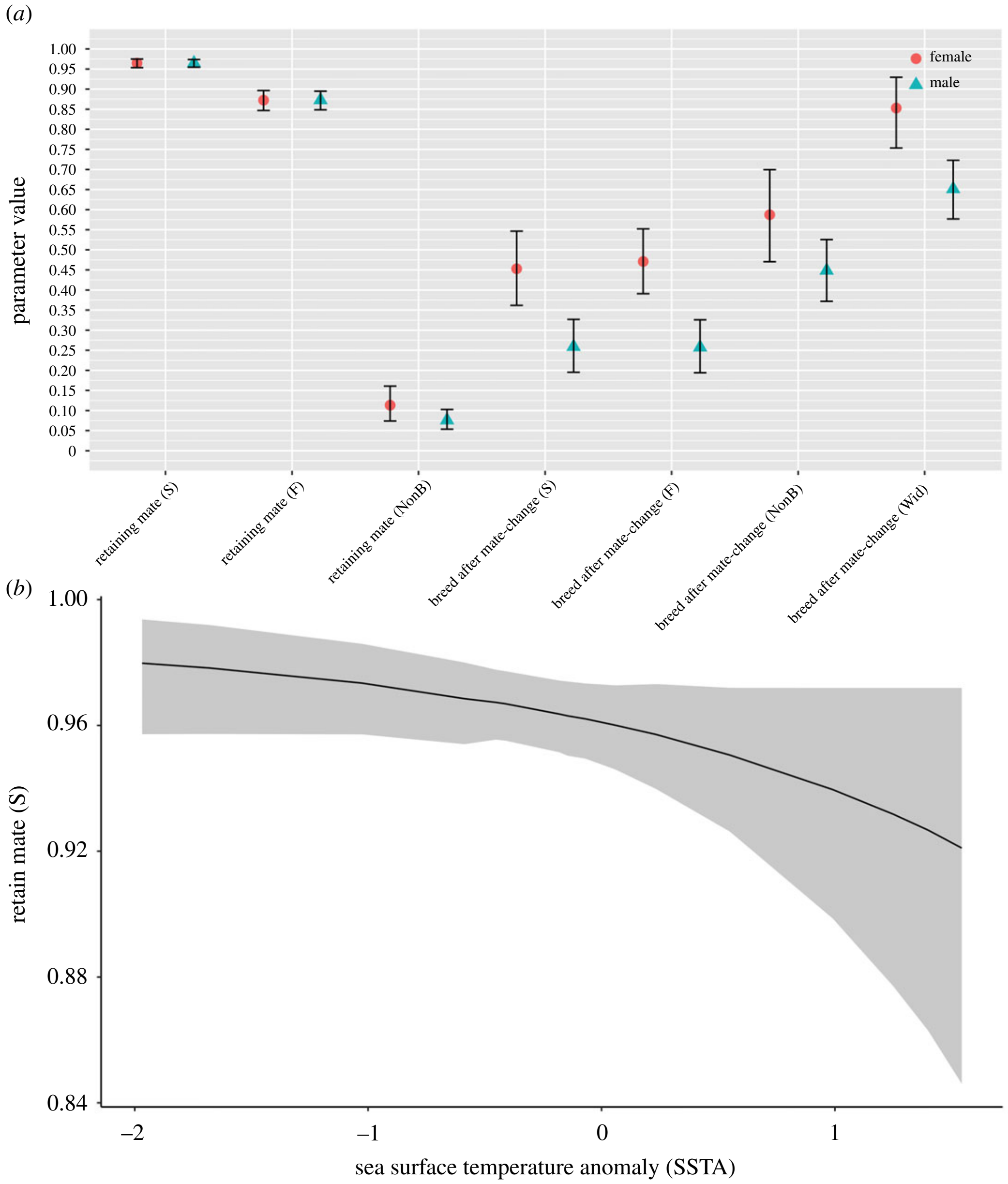

Figure 3. (*a*) The probabilities of retaining the previous mate (breed$_{STAY}$ in the text) for successful (S), failed (F) and non-breeding (NonB) individuals and the probabilities of breeding after mate-change (breed$_{SWITCH}$ in the text) for previously successful (S), failed (F) non-breeding (NonB) and widowed (Wid) birds estimated by the state space model. The parameters for females (dot) and males (triangle) are shown with the respective 95% credible interval, calculated as the 2.5th to the 97.5th quantile of each parameter posterior distributions. (*b*) The effect of standardized sea surface temperature anomaly on the probability of retaining the previous mate for previously successful females. The shaded area shows the 95% credible interval, ranging from the 2.5th to the 97.5th quantile of the parameter posterior distribution. (Online version in colour.)

knowledge, this is the first empirical evidence in support of the habitat-mediated hypothesis tested under a temporal perspective, revealing the effects of temporal environmental variability on the prevalence of divorce in a socially monogamous population. Owing to the particularly advantageous features of our study population (see above and the electronic supplementary material), the validity of the assumption of exact state assignment in our multi-event SSM framework is strongly supported. Nevertheless, given its flexibility, the analytical framework developed in this study can be extended to other species by incorporating a probabilistic state assignment formulation to better account for uncertainty in the assignment of widowed and non-breeding individuals. In turn, our methodology promises to be widely applicable to investigate the drivers and the consequences of divorce in other study systems and, more in general, to address ecological questions on the effects of the environment on the breeding processes in a wide range of other socially monogamous species.

(a) (Hp 1) Reproductive failure triggers divorce

In line with the predictions for long-lived species with stable nesting sites [3,11], the Falklands black-browed albatross population showed high levels of mate fidelity and a relatively low average yearly divorce rate (3.7%). Nevertheless, divorces occurred every year and all our models consistently indicated that failed pairs were less likely to remain together than successful pairs. Moreover, as shown by the GLMM results, the timing of failure is an important element in divorce. In fact, individuals failing during incubation were five times more likely to divorce their partner than those that failed after hatching or that were successful. Early failures may be indicative of an infertile or incompatible mate [29]. Moreover, as the potentially detrimental effects of the environmental stochasticity on breeding processes accumulate and intensify throughout the different phases of the breeding cycle, the mate parental ability is more clearly signalled during the early breeding stages [30].

The SSM results indicate that, after mate-change, the probability of breeding with a new mate is consistently higher in females than in males, for all the states considered. Furthermore, even if to a limited extent, females were more likely to improve their breeding success after divorce (but not after widowing) compared to males (electronic supplementary material). Collectively, these findings all support the hypothesis that divorce is an active decision initiated by females, the 'choosing' sex in birds [7,31–33], triggered by breeding failure. This has been suggested in previous studies and classically recognized in the ecological literature, and is consistent with our results on the comparatively higher reproductive benefits in females, both in terms of a higher probability of finding a new mate and a relatively higher improvement in breeding success. The marginally higher survival rate of males compared to females quantified by our SSM (electronic supplementary material) may be indicative of a higher availability of males. Nevertheless, the higher cost of divorce for males (i.e. lower probability of finding new mates, see also paragraph below, and minimal or no improvements in breeding success) and the non-significant correlation found between the yearly number of available widows and the yearly divorce rate suggests that males are likely less prone to initiate divorce than females. Our conclusion on females being the 'choosing' sex should therefore be robust to a potential slight sex bias.

After mate-change, males are less likely to breed with a new partner than females. This is true particularly for divorced males, which are probably poor quality individuals and have a lower probability of breeding with a new mate compared to widowed males [31]. Conversely, females that did not retain their mate (particularly those in the non-breeding and widowed states) had the highest probability of breeding with a new mate; however, widowed birds pay the forced mate-change costs with a lower reproductive success (electronic supplementary material), probably because they did not actively choose to divorce their partner and therefore do not gain the benefits of choosing a new, better mate [3].

(b) (Hp 2) Divorce varies in time and is affected by the environment

The albatross population divorce rate showed a marked inter-annual variability. All our models (which focussed both on population-level rates, such the quasi-binomial GLM, and also on individual-level responses, such as the GLMMs and SSMs) were consistent in showing that this variability is directly modulated by changes in the environment. Our findings show that the environment does not exclusively affect divorce through an indirect pathway by shaping the population productivity. Owing to the analytical depth attained by our analysis, the results of the individual based models (which simultaneously assessed the role of intrinsic and environmental covariates) highlighted that the effects of environmental variability on divorce are in fact not limited to an indirect link mediated by changes in demographic rates. In particular, our models showed an increase in divorce (higher divorce rate at the population level, higher probability of divorce and lower probability of retaining the previous mate at the individual level) in years of warm SSTAs. High SSTAs negatively affect marine primary and secondary productivity [21,34,35], reducing food availability for seabirds via bottom-up processes [21,36–38]. In the Falklands black-browed albatross population, high SSTA was found to negatively affect breeding rate and breeding success [17].

Our findings strongly support the habitat-mediated hypothesis: presumably harsh conditions linked to high SSTA play a disruptive role in the population breeding processes and lead to a higher divorce rate. As shown by our GLMM, breeding failure, particularly at early stages of the reproductive period, is the main trigger of divorce; however, together with the effects of the previous breeding score, there is a clear and significant effect of SSTA in increasing the probability of divorce. Crucially, when focussing on the probability of retaining the previous mate, the SSM results suggest that, while the effect of SSTA on males and on previously failed and non-breeding females was not conclusive, it is the females in a previously successful relationship that are mostly affected by the environmental harshness. Hence, the emerging interpretation from the evidence obtained is as follows: while breeding failure is the main trigger of divorce for unsuccessful females, the environment acts upon the ones that, based on the 'win–stay, lose–switch' process, should have remained with their previous mate. The alternative hypothesis of an environmental 'discounting' of breeding failures in resource poor years [6] is not supported by our results. In fact, the prediction of this hypothesis is that harsh conditions would decrease the probability of divorce for previously failed breeders, whereas there is no predicted effect of the environment on previously successful birds. Instead, the results of our GLMM show a clear, significant increase in the probability of divorce as SSTA increased (electronic supplementary material), affecting breeding females regardless of their previous breeding score (i.e. the interaction term between environmental covariates and previous breeding score was not retained as significant in our GLMM). In this study, we cannot formally investigate the existence of ecological cross-overs [16]. However, given the longevity of albatrosses and the benefits arising from long-term relationships, it is reasonable to assume that changes in the sexual selection process would mainly affect the levels of extra-pair mating rather than divorce [16].

Various non-mutually exclusive mechanisms might underpin the environmental effects on divorce. In seabirds, bad conditions determine higher costs of reproduction and higher breeding effort [39], causing individuals to arrive to the following breeding season later (i.e. affecting the phenology) or in a poorer physiological state [40,41]. Environmental effects on the breeding phenology of migratory species might cause asynchronous arrivals to the breeding ground between pair members [42,43], ultimately promoting divorce [44]. The higher mortality rate caused by environmental harshness can also decrease the costs of mate-change by increasing the availability of alternative mates, i.e. the widowed individuals [11]; however, in our monitored population, widowed availability did not correlate with divorce rate.

In resource-poor seasons, the deleterious effects of harsh environmental conditions might misinform the decision-making processes of individuals (and in particular of females, the 'choosy' sex), potentially leading them to attribute their poorer state to a poorer performance of their partners. Thus, a potential mechanistic pathway linking environment, mate choice and divorce rate might be underpinned by physiological stress. Stress hormones are key mediators of breeding and sexual selection processes [45]. Recent experimental evidence in finches revealed that 'unsatisfied' females in relationships with sub-optimal partners had a level of corticosterone that was three to four times higher than that observed in females paired with preferred mates [46]. Together with this direct response, breeding with sub-optimal mates might increase, in females, the breeding investment and physiological stress levels to compensate for the poor mate performance [47]. Crucially, in seabirds, hard environmental conditions and food shortage are associated with higher levels of circulating stress hormone corticosterone [48,49]. Thus, after a difficult resource-poor breeding season, the greater effort and higher breeding investment can lead stressed females to disrupt the bond with their previous mate and look for a new one, even if previously successful.

5. Conclusion

Our work provides, to our knowledge, the first evidence of a significant influence of the prevailing environmental conditions on the prevalence of divorce in a long-lived socially monogamous population. This conclusion is probably not only relevant to our study system. We argue that investigating divorce adopting a temporal perspective may provide critical insight into the role of the environment on divorce in other socially monogamous avian and mammalian populations. Focussing our analytical lens both at the population level (yearly divorce rate) and also at the fine scale individual level (probability of divorce and probability of retaining the previous mate), all the modelling techniques adopted consistently indicated that divorce is triggered by breeding failure, but, crucially, that it is also promoted by environmental harshness. The mate familiarity arising from socially monogamous bonds and the improved coordination between the members of a pair is often essential for successfully raising healthy offspring in the variable, dynamic marine environments exploited by seabirds [9,50]. Hence, in light of the dramatic extent of the current climatic changes, the environmentally driven disruptions of the breeding processes of socially monogamous populations might represent an overlooked consequence of global change, with repercussions on demography and population dynamics.

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

Data accessibility. The supporting data and R scripts to reproduce the analysis are available from the Figshare digital repository: https://figshare.com/articles/online_resource/Data_analysis__Environmental_variability_directly_affects_the_prevalence_of_divorce_in_monogamous_albatrosses_/14696451 [51].

Authors' contributions. F.V.: conceptualization, data curation, formal analysis, investigation, methodology, resources, writing—original draft, writing—review and editing; J.P.G.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—review and editing; P.M.L.: formal analysis, methodology, resources, supervision, writing—review and editing; A.K.: data curation, investigation, methodology, resources, writing—review and editing; P.C.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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