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Causes and consequences of pair-bond disruption in a sex-skewed population of a long-lived monogamous seabird

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Abstract

Many animals form long-term monogamous pair bonds, and the disruption of a pair bond (through either divorce or widowhood) can have significant consequences for individual vital rates (survival, breeding, and breeding success probabilities) and life-history outcomes (lifetime reproductive success [LRS], life expectancy). Here, we investigated the causes and consequences of pair-bond disruption in wandering albatross (*Diomedea exulans*). State-of-the-art statistical and mathematical approaches were developed to estimate divorce and widowhood rates and their impacts on vital rates and life-history outcomes. In this population, females incur a higher mortality rate due to incidental fishery bycatch, so the population is male-skewed. Therefore, we first posited that males would show higher widowhood rates negatively correlated with fishing effort and females would have higher divorce rates because they have more mating opportunities. Furthermore, we expected that divorce could be an adaptive strategy, whereby individuals improved breeding success by breeding with a new partner of better quality. Finally, we posited that pair-bond disruptions could reduce survival and breeding probabilities owing to the cost of remating processes, with important consequences for life-history outcomes. As expected, we showed that males had higher widowhood rates than females and females had higher divorce rates in this male-skewed population. However, no correlation was found between fishing effort and male widowhood. Secondly, contrary to our expectation, we found that divorce was likely nonadaptive in this population. We propose that divorce in this population is caused by an intruder who outcompetes the original partner in line with the so-called forced divorce hypothesis. Furthermore, we found a 16.7% and 18.0% reduction in LRS only for divorced and widowed males, respectively, owing to missing breeding seasons after a pair-bond disruption. Finally, we found that divorced individuals were more likely to divorce again, but whether this is related to specific individual characteristics remains an important area of investigation.

KEYWORDS
bycatch, capture–mark–recapture, divorce, life-history outcomes, Markov chain models, sex-biased, vital rates, wandering albatross, widowhood

INTRODUCTION

A wide range of species form socially monogamous pair bonds that are maintained during one or more consecutive breeding seasons (Reichard & Boesch, 2003). This is mostly common in birds, with an estimated 90% of avian species being socially monogamous (Emlen & Oring, 1977). Breeding with the same partner can reduce the time and energy required to form a new pair bond and improve familiarity between partners, which could ultimately enhance vital rates in terms of survival, breeding, and breeding success probabilities (Black, 2001; Culina et al., 2020; Griggio & Hoi, 2011; Leach et al., 2020; Sánchez-Macouzet et al., 2014; van de Pol et al., 2006). Pair-bond disruption happens through either widowhood or divorce. Widowhood is a result of a partner's death, while divorce happens for both partners simultaneously when at least one of them breeds with a new partner. When investigating the causes and consequences of pair-bond disruption, few studies have included divorce and widowhood simultaneously (Bried et al., 2003; Culina, Lachish, & Sheldon, 2015; Ens et al., 1993; Forslund & Larsson, 1991). However, it is important to include both divorce and widowhood as two mutually exclusive mechanisms of pair-bond disruption since they may lead to different consequences for vital rates and life-history outcomes.

The frequency of pair-bond disruption has been shown to be higher in sex-biased populations because differences in mortality rates between sexes can result in a higher widowhood rate for one sex and increased mate choices for the less abundant sex, leading to a higher divorce rate (Grant & Grant, 2019; Liker et al., 2014). Moreover, in a population with skewed operational sex ratio (OSR), the more abundant sex may have fewer opportunities to establish a new pair bond after a pair-bond disruption, leading to a reduced lifetime reproductive success (LRS). Hence, understanding mechanisms of pair-bond disruption is particularly relevant in sex-biased populations.

Divorce can be an adaptive strategy, but widowhood is not (Black, 1996; Choudhury, 1995; Culina, Lachish, & Sheldon, 2015; Jeschke & Kokko, 2008). As an adaptive strategy, individuals divorce to improve their reproductive performance or avoid future decline of breeding success by breeding with a new partner of better quality. In this case, the prospect of future reproductive success may influence divorce probability, with a higher frequency of divorce observed among young individuals (Naves et al., 2006; Pampus et al., 2005).

Divorce may also arise from other nonadaptive mechanisms. For example, divorce can result from a stochastic disturbance, such as temporary separation due to harsh environmental conditions, and from interference by an intruder who outcompetes the original partner. The latter form of divorce is referred to as a *forced divorce* hypothesis (reviewed in Choudhury [1995]). This hypothesis has also been supported in empirical studies (e.g., common guillemots [*Uria aalge*], Alpine marmots [*Marmota marmota*], and Eurasian beavers [*Castor fiber*]) (Jeschke et al., 2007; Lardy et al., 2011; Mayer et al., 2017).

Regardless of the causes of pair-bond disruption, divorce and widowhood may affect vital rates and life-history outcomes. For example, once divorced or widowed, individuals may skip several breeding seasons before bonding with a new partner, which can have significant effects on LRS in monogamous species (Jouventin et al., 1999; Sogabe et al., 2007). McNamara and Forslund (1996) suggested that the cost of pair-bond disruption is much lower in long-lived species than short-lived species because they have more future reproductive opportunities. However, the cost of staying single can also be substantial in long-lived species because they often have low fecundity and spend a long time establishing an operational pair bond (Bried et al., 2003; Jouventin et al., 1999; Jouventin & Bried, 2001). For example, the reproductive costs of remating appeared substantial in wandering albatross (*Diomedea exulans*) because it can take 3.2 and 2.3 years of display activities before starting to mate and breed again for males and females, respectively, which results in a reduction in LRS each time a pair-bond disruption occurs (Jouventin et al., 1999).

Moreover, in long-lived monogamous species maintaining long-term pair-bond relationships, newly bonded partners tend to experience an immediate decrease in breeding success, which is referred to as *the syndrome of the first-year bond* (Naves et al., 2007). This immediate cost of reproduction may conceal long-term changes in the breeding success of long-lived species. Therefore, understanding the prolonged impacts of pair-bond disruption requires monitoring breeding success over multiple breeding seasons (Choudhury, 1995; Culina, Lachish, & Sheldon, 2015). However, no study to date has tracked changes in breeding success over extended periods after a

pair-bond disruption in wild long-lived species (but see van de Pol et al., [2006] for an experimental approach).

In addition to the reproductive consequences of pair-bond disruption, searching for a new partner can be energy- and time-consuming, leading to an increased risk of mortality (Nicolai et al., 2012; Culina, Radersma, & Sheldon, 2015; Jankowiak et al., 2018). Lower survival rates from higher reproduction cost or predation risk following a pair-bond disruption can further reduce the remaining life expectancy of an individual at a given stage. Hence, the survival cost of pair-bond disruption can be substantial in long-lived species compared with short-lived species (McNamara & Forslund, 1996). To our knowledge, only a handful of studies have analyzed the direct impacts of pair-bond disruption on survival including research projects on black brant (*Branta bernicla nigricans*), great tit (*Parus major*), black tit (*Cyanistes caeruleus*), and European blackbirds (*Turdus merula*) (Culina, Radersma, & Sheldon, 2015; Jankowiak et al., 2018; Leach et al., 2020; Nicolai et al., 2012). All the studies showed negative impacts of pair-bond disruption through either divorce or widowhood on survival.

Here, we analyzed the causes and consequences of pair-bond disruption in a long-lived monogamous seabird, the wandering albatross breeding on Crozet Island, sub-Antarctica, using a long-term capture–mark–recapture data set since 1967. Wandering albatrosses form long-lasting pair bonds (Bried et al., 2003), and in this population, females experience a higher fishery-induced bycatch mortality resulting in a high proportion of widowed males and a male-skewed OSR (Jouventin et al., 1999; Weimerskirch, 2018; Weimerskirch et al., 1997, 2005; Weimerskirch & Jouventin, 1987). We estimated divorce and widowhood rates simultaneously and investigated both the short- and long-term effects of pair-bond disruptions on individual vital rates and life-history outcomes using diverse approaches, including multievent capture–mark–recapture (MECMR), absorbing Markov chains (AMCs), and generalized linear mixed model (GLMM). We posited that (1) males have a higher widowhood probability due to sex-biased mortality correlated with fishing effort and that females have a higher divorce rate because of a male-skewed population; (2) divorce may be adaptive, leading to improved breeding success; and (3) pair-bond disruption affects individual vital rates and life-history outcomes (Table 1).

MATERIALS AND METHODS

Patterns of pair-bond disruption were analyzed by estimating rates of divorce and widowhood. To understand the causes of pair-bond disruption, we analyzed the impacts of fisheries and reproductive success on pair-bond disruption rates. Then we investigated the consequences of pair-bond disruption on vital rates, including survival and breeding probabilities and life-history outcomes, including life expectancy and LRS, and state occupancy times (breeding intervals, expected time to next divorce).

Pair-bond disruption rates and vital rates were estimated using MECMR models accounting for imperfect detection. The impacts of fishing efforts on pair-bond disruption rates were tested using fishing efforts as covariates in MECMR models. Then we characterized life-history outcomes and occupancy times using an AMC framework. These two methodologies (MECMR and AMC) included only transitions of living individuals in the life cycle of a species described in the section "Life cycle." A species life cycle can be described by structuring the population into individual states, such as age or breeding states (breeder vs. nonbreeder) (Caswell, 2011). In a life cycle, individuals move from state j to state i over the course of one time step (here a year) with specific transition probabilities.

Hence, we first developed a new MECMR model to estimate vital rates and probabilities of divorce and widowhood simultaneously using individual capture–mark–recapture life histories; see the sections "Study species" and "Structure of multievent capture–mark–recapture (MECMR) model." Second, we developed an AMC, which is a stochastic process that undergoes transitions from one state to another where each state can reach a state that, once entered, cannot be left, known as *an absorbing state*, such as a death state. The AMC was parameterized using the vital rates and pair-bond disruption rates estimated from the MECMR models (section "Capture–mark–recapture model to estimate pair-bond disruption and vital rates"). Finally, we tested whether divorce is an adaptive strategy using a GLMM framework to assess the causes (section "Causes of divorce") and consequences (section "Consequences of divorce") of divorce.

Study species

Our study population of wandering albatrosses breeds on Possession Island, Crozet (46°24′ S 51°46′ E). Wandering albatrosses forage in sub-Antarctic and subtropical waters between latitudes 30° S and 60° S while breeding (Weimerskirch et al., 2012) and show a wide distribution in the Southern Ocean during the nonbreeding period (Weimerskirch et al., 2015), mainly feeding on fish and squid (Weimerskirch et al., 1986). Wandering albatrosses are generally regarded as biennial breeders because of their long chick-rearing period (up to 280 days), so most individuals take a sabbatical year at sea after each breeding season

TABLE 1 Hypotheses and expectations

Expectation	Method
1. Rates of widowhood and divorce in a male-skewed population	
(1a) Males have a higher widowhood rate than females due to the sex-biased mortality	MECMR, *Capture–mark–recapture model to estimate pair-bond disruption and vital rates*
(1b) Females have higher divorce rate than males because of male-skewed population	MECMR, *Capture–mark–recapture model to estimate pair-bond disruption and vital rates*
(1c) Male widowhood rates are proportional to fishing effort due to sex-biased bycatch mortality	MECMR using fishing effort as covariates, *Causes of widowhood: Fishery covariates in MECMR model*
2. Divorce is an adaptive strategy in terms of breeding success	
(2a) Divorce is triggered by low reproductive success with previous partner but no such pattern in widowhood By short-term breeding success with previous partner By long-term breeding success within entire pair-bond duration with previous partner	GLMM, *Causes of divorce*
(2b) Divorce leads to improvement of breeding success but no such pattern in widowhood Higher short-term breeding success with new partner Higher long-term breeding success with new partner during entire pair-bond duration	GLMM/GLM, *Consequences of divorce*
3. Impact of pair-bond disruption on vital rates and life-history outcomes	
(3a) Annual vital rates Survival: Individuals experiencing pair-bond disruption have lower survival than individuals staying with same partner Breeding probability: Single divorced and widowed individuals have lower breeding probabilities due to extended remating processes Breeding success: Divorced and widowed individuals may have lower breeding success after bonding with new mate due to "syndrome of first-year bond"; divorced individuals may also have higher breeding success due to adaptive strategy compared with widowed individuals and individuals staying with same partner	MECMR, *Capture–mark–recapture model to estimate pair-bond disruption and vital rates*
(3b) Life-history outcomes in male-skewed population Females have increased lifetime reproductive success (LRS) after divorce but no change after widowhood, while males have decreased LRS after divorce and widowhood due to missed breeding opportunities compared with individuals staying with same partner Individuals experiencing pair-bond disruption have lower life expectancy due to cost of survival	AMC, *Life-history outcomes*

Note: The methodological approach and section are specified: AMC, absorbing Markov chains; GLM, general linear model; GLMM, generalized linear mixed model; MECMR, multievent capture–mark–recapture.

(Tickell, 1968). A typical timeline of successive visits to check the identity of individuals and wandering albatross breeding cycle is presented in Figure 1. The two parents of a pair bond perform similar roles of parental care during reproduction by alternating foraging trips at sea. Both female and male provide long and extensive parental care for a single offspring, from nest formation until fledging, and invest a large amount of time in mate choice and pair-bond formation (Tickell, 2013). Moreover, wandering albatrosses display extreme life-history traits such as late sexual maturity, low fecundity, and long lifespan. Individuals only start breeding at the ages of 7–9 (Weimerskirch, 1992) and lay one egg at each breeding attempt (Barbraud & Weimerskirch, 2012).

In the meantime, wandering albatrosses are listed as Vulnerable (International Union for Conservation of Nature [IUCN] red list) because they are threatened by incidental fishery bycatch (Weimerskirch & Jouventin, 1987). Population decreases have been documented in most large colonies, with a marked decline during the 1970s and 1980s (Weimerskirch et al., 1997). In Crozet, accidental capture by long-line fisheries in the 1970s and 1980s was the major threat affecting wandering albatrosses survival leading to a high proportion of widowed individuals in the population (Jouventin et al., 1999; Weimerskirch et al., 2005).

Recent mitigation measures have been implemented to reduce bycatch mortality, and some wandering

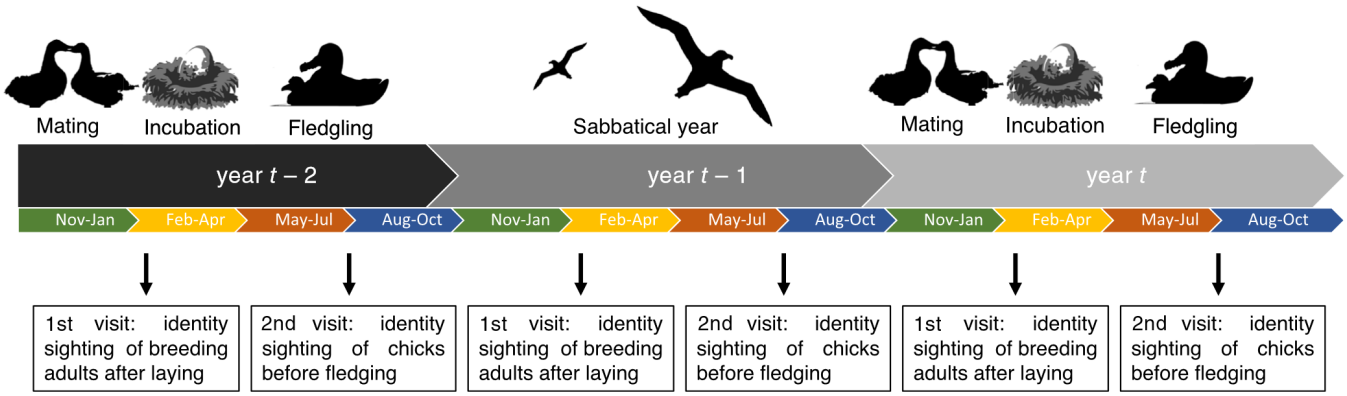

FIGURE 1 Successive visits to check the identity of individuals (banding sightings) and a typical timeline of wandering albatross breeding cycle. The definition of year here follows the breeding cycle rather than chronological order. In this population of Crozet, prelaying courtship and pair-bond reformation, nest building and copulation occur from mid-November to mid-December. For the wandering albatross, breeding pairs usually separate at the end of a breeding season at $t - 2$ and spend a year off at sea in the following year $t - 1$ as postbreeding adults foraging in different sectors (Weimerskirch et al., 2014). After a sabbatical year, these postbreeding adults return to the colony at year t and start another breeding season. Some individuals may reproduce every year, but that event is uncommon in this population. There are two censuses for breeding adults and fledglings each year. Specifically, the rings of breeding adults are checked just after egg laying during several successive visits in order to determine the identity of the partners, and all chicks are ringed just before fledging. At fledging, breeding performance is determined for most individuals. Breeding individuals (i.e., those laying an egg) are classified as successful breeders when they fledge a chick, otherwise they are failed breeders. Colors indicate austral spring (green), summer (yellow), autumn (orange), and winter (blue)

albatross populations are recovering. Mitigation measures were first introduced voluntarily in the late 1980s. The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) introduced compulsory highly effective mitigation from 2003, and the Indian Ocean Tuna Commission (IOTC) implemented specific resolutions from 2010 that are not compulsory in subtropical waters. These changes in fishing practices, as well as the relocation of fishing grounds for some tuna species (Weimerskirch et al., 1997), might end up contributing to the recovery of the Crozet population starting in the mid-1980s (Barbraud et al., 2013; Delord et al., 2008).

Banding (unique ring numbers on the leg) on Possession Island started in 1960, and since 1966, a capture–mark–recapture program has been undertaken annually between December and April. The identities of breeding birds were checked in January and February (three to four visits per nest), starting immediately after egg laying, and all chicks were ringed with stainless-steel rings in September and October before fledging (Figure 1). At fledging, breeding success was determined. Each year, new individuals found in the colony were ringed and their breeding status determined. Sex was determined using morphometric measurements and genetic sexing (Weimerskirch et al., 2005). In this study, we used the data of breeding adults identified from 1967 through 2011, and this yielded a total number of 1677 female and 1802 male life histories in our data set.

Life cycle

A life cycle can be described by structuring the population into individual states. For wandering albatrosses, the population was structured into individual states depending on their pair-bond status (i.e., bonding with a new partner or mating with the same partner than the previous season) and breeding status (i.e., nonbreeder or breeders), and we included transitions of living individuals from one state to another. Eight individual states were defined in the population including a dead state (Table 2). Individuals that are breeders in year t can breed with the same partner (S) from the previous breeding attempt, and they can also breed with a new partner after a divorce (ND) or widowhood (NW). Hence, we included states of individuals paired with a new partner versus paired with the same partner from the previous breeding attempt, and we distinguished divorce from widowhood by modeling whether the focal individual's partner from the last breeding event was dead or not. Since more than 80% of wandering albatrosses breed biennially (Tickell, 2013), they were allowed to enter a postbreeding state. We included postbreeders after breeding with the same partner (Post-S) and breeding with a new partner (Post-N). Divorced (D) and widowed (W) individuals are nonbreeding individuals that lost their partners at the last breeding attempt. Hence, nonbreeders are Post-S, Post-N, D, and W individuals that skip breeding in the current breeding season and can be divorced,

TABLE 2 Definitions of states in our MECMR model

	State	Definition
1	**S**	Breeding with same partner
2	**ND**	Breeding with new partner following divorce
3	**NW**	Breeding with new partner following widowhood
4	**Post-S**	Previously S at $t-1$, skipping breeding at t
5	**Post-N**	Previously ND or NW at $t-1$, skipping breeding at t
6	**D**	Divorced individual skipping breeding at t
7	**W**	Widowed individual skipping breeding at t
8	**Dead**	...

Notes: The model was structured by states based on individual pair-bond status (staying with the same/new partner, divorced or widowed) and breeding status (breeding vs. nonbreeding). The transitions of individuals between different states occur from the end of the breeding season at $t-1$ to the next breeding season at t, and the time step is 1 year. Individuals can skip breeding at season t, so their previous partner is defined as the partner at their last breeding season, $t-k$. State acronyms appear in bold.

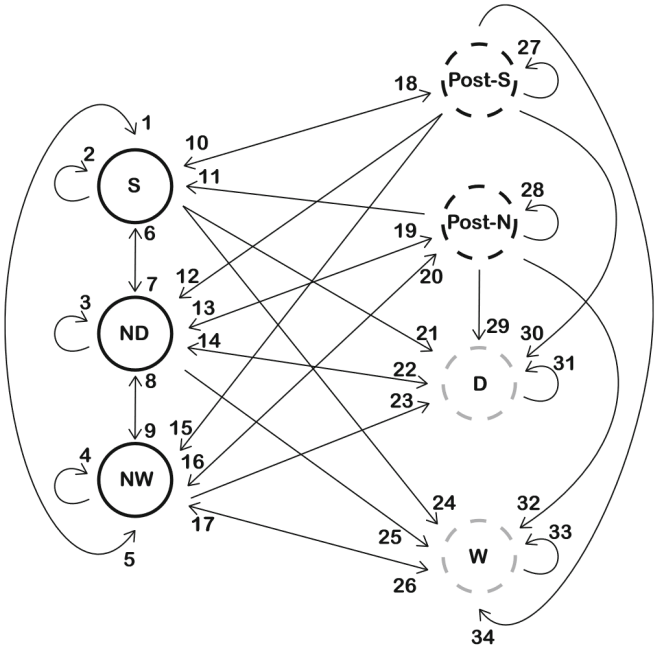

FIGURE 2 Life-cycle graph for wandering albatrosses, illustrative figure of transitions of living individuals from one state to another to estimate pair-bond disruption rates and vital rates. Seven possible states are defined in Table 2. States S, ND, and NW with solid circles indicate breeders in year t. States Post-S, Post-N, D, and W with dashed circles are nonbreeders in year t. The dead state (No. 8) is not shown. Solid circles indicate breeders, and dashed circles represent nonbreeders in year t. Lighter circles indicate individuals that are not in a pair-bond relationship. Transitions between pair status from year $t-1$ to year t are conditional on survival, widowhood (survival of the partner from $t-1$ to t), breeding, and divorce. Transitions between states are numbered and described in Table 3

widowed, or in a sabbatical year after breeding with their partners. Although Post-S and Post-N are nonbreeders in their sabbatical year, they are still in a long-term pair-bond relationship with their partners, while divorced and widowed individuals are not committed in a pair-bond relationship.

Individuals move from state j to state i during one time step (here a year), and these transitions shown in Figure 2 depend on vital rates and pair-bond disruption rates of individuals, including (1) the survival probability from $t-1$ to t of the focal individual, (2) the widowhood probability from $t-1$ to t of the focal individual, (3) the breeding probability in year t of the focal individual, and (4) the divorce probability in year t of the focal individual (i.e., the focal individual or its partner is breeding with a new partner).

Pair-bond disruption rates are conditional probabilities. For example, the transition probability from Post-S to W shown as Post-S → W in Table 3 is $s_j \times w_j \times (1-\beta_j)$, where s_j is the probability that Post-S individuals survive from $t-1$ to t; w_j is the probability that they become widowed conditional on their own survival, and $1-\beta_j$ is the probability they skip breeding in year t conditional on survival and widowhood probabilities. Another example to illustrate divorce is the transition from Post-S to ND shown as Post-S → ND in Table 3. Post-S individuals survive from $t-1$ to t and do not lose their previous partner through death with a probability $1-w_j$, then with a probability β_j they breed in year t but with a different partner with a probability d_j. Thus, the transition probability of Post-S → ND is $s_j \times (1-w_j) \times \beta_j \times d_j$.

Capture–mark–recapture model to estimate pair-bond disruption and vital rates

Structure of multievent capture–mark–recapture (MECMR) model

To estimate pair-bond disruption rates, we built upon a MECMR model developed in Veran and Beissinger (2009) and Culina et al. (2013), which included whether an individual was breeding with the same or a different partner from the previous reproductive occasion (i.e., pair-bond status). Here we extended this model to include both divorce and widowhood simultaneously. Bienniality was included in the model structure by adding the post-non-breeding states Post-S and Post-N (Table 2). Hence, the population was structured into individual states depending on their pair-bond and breeding status for each sex separately. To determine the pair-bond status of initial states, individuals entered the model at their second breeding attempt

TABLE 3 Transition probabilities between pair-bond status

Arrow number	State transition	Transition probability
1	**NW → S**	$s_3 \times (1 - w_3) \times \beta_3 \times (1 - d_3)$
2	**S → S**	$s_1 \times (1 - w_1) \times \beta_1 \times (1 - d_1)$
3	**ND → ND**	$s_2 \times (1 - w_2) \times \beta_2 \times d_2$
4	**NW → NW**	$s_3 \times w_3 \times \beta_7$
5	**S → NW**	$s_1 \times w_1 \times \beta_7$
6	**ND → S**	$s_2 \times (1 - w_2) \times \beta_2 \times (1 - d_2)$
7	**S → ND**	$s_1 \times (1 - w_1) \times \beta_1 \times d_1$
8	**NW → ND**	$s_3 \times (1 - w_3) \times \beta_3 \times d_3$
9	**ND → NW**	$s_2 \times w_2 \times \beta_7$
10	**Post-S → S**	$s_4 \times (1 - w_4) \times \beta_4 \times (1 - d_4)$
11	**Post-N → S**	$s_5 \times (1 - w_5) \times \beta_5 \times (1 - d_5)$
12	**Post-S → ND**	$s_4 \times (1 - w_4) \times \beta_4 \times d_4$
13	**Post-N → ND**	$s_5 \times (1 - w_5) \times \beta_5 \times d_5$
14	**D → ND**	$s_6 \times \beta_6$
15	**Post-S → NW**	$s_4 \times w_4 \times \beta_7$
16	**Post-N → NW**	$s_5 \times w_5 \times \beta_7$
17	**W → NW**	$s_7 \times \beta_7$
18	**S → Post-S**	$s_1 \times (1 - w_1) \times (1 - \beta_1) \times (1 - d_6)$
19	**ND → Post-N**	$s_2 \times (1 - w_2) \times (1 - \beta_2) \times (1 - d_7)$
20	**NW → Post-N**	$s_3 \times (1 - w_3) \times (1 - \beta_3) \times (1 - d_7)$
21	**S → D**	$s_1 \times (1 - w_1) \times (1 - \beta_1) \times d_6$
22	**ND → D**	$s_2 \times (1 - w_2) \times (1 - \beta_2) \times d_7$
23	**NW → D**	$s_3 \times (1 - w_3) \times (1 - \beta_3) \times d_7$
24	**S → W**	$s_1 \times w_1 \times (1 - \beta_7)$
25	**ND → W**	$s_2 \times w_2 \times (1 - \beta_7)$
26	**NW → W**	$s_3 \times w_3 \times (1 - \beta_7)$
27	**Post-S → Post-S**	$s_4 \times (1 - w_4) \times (1 - \beta_4) \times (1 - d_6)$
28	**Post-N → Post-N**	$s_5 \times (1 - w_5) \times (1 - \beta_5) \times (1 - d_7)$
29	**Post-N → D**	$s_5 \times (1 - w_5) \times (1 - \beta_5) \times d_7$
30	**Post-S → D**	$s_4 \times (1 - w_4) \times (1 - \beta_4) \times d_6$
31	**D → D**	$s_6 \times (1 - \beta_6)$
32	**Post-N → W**	$s_5 \times w_5 \times (1 - \beta_7)$
33	**W → W**	$s_7 \times (1 - \beta_7)$
34	**Post-S → W**	$s_4 \times w_4 \times (1 - \beta_7)$

Notes: Arrow number corresponds to transitions between each pair-bond status shown in Figure 2. s_j, w_j, β_j, and d_j are survival, widowhood, breeding, and divorce probabilities described in the section "Life cycle" and specified in Appendix S1: Section S1.1.

because we needed to determine whether they were breeding with the same previous partner or not.

The states were connected with 13 observation events shown in Appendix S1: Table S1 (Pradel, 2005; Pradel et al., 2008). Appendix S1: Section S1.1 details the state transitions and observation processes. To define the event "death," we treated an individual not observed at the colony for five consecutive years as dead, because the average probability of not observing a breeder for five consecutive years is 0.000001 for wandering albatrosses (Cornioley et al., 2017). Hence, we performed our analysis until 2011 to account for extra years of records that are necessary to determine the survival status of individuals. To define the event "divorce," we removed the birds with temporary divorce events, i.e., breed with another transient partner while their long-term partner skips

breeding (Weimerskirch et al., 2015). We also included uncertain events because states were not always recorded between 1967 and 1986 owing to the nonstandardized protocol. The field monitoring methods improved after 1986 (Barbraud & Weimerskirch, 2012). Thus, our MECMR model included uncertainties caused by imperfect observation processes through a series of conditional probabilities as a hidden Markov process. The models were run in E-SURGE Version 2.0 (Choquet et al., 2009) and E-SURGE code is available on the US Antarctic Program Data Center (USAP-DC) repository.

MECMR model selection

In our framework, the divorce of a pair bond affects two partners simultaneously, and the widowhood of a focal individual happens through the death of its partner. To address this statistical nonindependence among life histories, we followed the procedure developed in Culina et al. (2013) by applying the MECMR framework to capture histories of males and females separately. A step-down model selection was performed for each sex independently, and the two separate covariance matrices of the best supported models for females and males respectively are shown in Appendix S1: Section S2.1.3.

Currently, there is no test available to assess the goodness of fit (GOF) for multievent models. In Culina et al. (2013), a simplified model was used to test for GOF. Previous studies using simpler model structures without pair-bond status on the same data set suggested the validity of general assumptions in spite of slight overdispersion (Barbraud & Weimerskirch, 2012; Fay et al., 2018). Thus, we assumed our general assumptions fit the data set following the approach of Culina et al. (2013) and corrected the information criterion by overdispersion in the model selection step.

We started the model selection from the most general time-invariant model for which vital rates and pair-bond disruption rates were different for each state. The code to generate elementary matrices in MECMR models in E-SURGE GEPAT (generator of pattern of elementary matrices) was included in Data S1: mecmr.pat. Model selection was based on the Akaike information criterion (AIC) (Burnham & Anderson, 2002). In our model selection, we used AIC corrected by overdispersion, or quasi-AIC (QAIC) (Lebreton et al., 1992). The model with the smallest QAIC value was selected. When comparing the performance of two models with a QAIC difference lower than 2, we selected the model with fewer parameters (Lebreton et al., 2012). The model selection started with detection probabilities. We then modeled survival, widowhood, breeding, and divorce probabilities successively while keeping the parameter constraints as the best supported model from the previous step. During the model selection, we tested state dependence and temporal variations in the pair-bond disruption and vital rates. Detailed model selection processes are presented in Appendix S1: Section S2.1.1.

Constraints on MECMR model structure

Given the complexity of our models, and to ensure the identifiability of all parameters, we added several constraints (see Appendix S1: Section S1.2 for details). Parameters that were estimated at the boundary or not identifiable were grouped with other identifiable parameters by states during the model selection (see Appendix S1: Section S1.2.1 for details). If a parameter was grouped with other parameters, the parameter was removed from the list of mathematical parameters, and QAIC was calculated based on the number of mathematical parameters (Choquet et al., 2009). Temporal constraints applied to period parameter estimates were either defined chronologically or based on trends of population abundance (Appendix S1: Section S1.2.2). Considering a higher level of uncertainties shown in estimates before 1986 (Appendix S1: Figures S6–S9), here we only present the average estimates between 1986 and 2011. To obtain averaged estimates and their confidence intervals, we ran four distinct models, where each type of parameter (survival, widowhood, breeding, and divorce rates) was time-constant while the structure of the other parameters was kept the same as the best supported model (hence, potentially time-varying).

Estimates of breeding success

Because the detection is close to one for breeders, the probability of breeding success was estimated separately depending on whether an individual was breeding with the same partner (S), with a new partner after divorce (ND), or with a new partner after widowhood (NW) in year *t*. The estimates were calculated by averaging the breeding success according to the pair-bond status of an individual.

Causes of widowhood: Fishery covariates in MECMR model

To test whether long-line fishery bycatch influences survival probability and leads to pair-bond disruption, we used fishery intensity (i.e., fishing effort) as a covariate for the entire study period (1967–2011). Numerous high-seas pelagic long-line fleets targeting tuna and tunalike species in the Southern Indian Ocean overlap with the

foraging distribution of wandering albatross (Tuck et al., 2003). Fishing effort near the Crozet archipelago reached its peak in the mid-1980s and declined notably afterward.

The distributions of both long-line fishery and wandering albatrosses showed distinct spatial and temporal dynamics during our study period. Postbreeding male wandering albatrosses are more dispersed and extensively distributed poleward, while postbreeding female wandering albatrosses are more restricted around Possession Island (Weimerskirch et al., 2014). During the breeding season, both males and females are restricted around Possession Island, while females forage more toward the north (Weimerskirch et al., 2014).

Fishing effort was defined as number of hooks deployed between December, the start of the breeding season, and the end of November of the following year in foraging grounds of wandering albatrosses (see Appendix S1: Figure S3 for distribution of breeding and nonbreeding foraging grounds). Fishing effort was generated from monthly reported long-line fishing effort data (numbers of hooks deployed) in $5^\circ \times 5^\circ$ spatial cells freely available from the Indian Ocean Tuna Commission (IOTC) https://www.iotc.org/documents/ce-longline accessed April 2019 (CE longline | IOTC). Fishing effort within each foraging ground showed substantial temporal variation during our study period (1967–2011) (see time series of fishing efforts in Appendix S1: Figure S4).

To detect the temporal variations of survival and widowhood explained by long-line fishery bycatch mortality, we applied the analysis of deviance (ANODEV) approach (Grosbois et al., 2008; Lebreton et al., 2012). Fishing efforts on breeding and postbreeding foraging grounds were modeled additively based on the selected model with the lowest QAIC. To calculate the ANODEV statistics, following the procedure in Lebreton et al. (2012), a series of models based on the best supported model (from the section "MECMR model selection") was built to analyze the relationship between fishery and probabilities of survival and widowhood.

Causes and consequences of divorce

To test hypothesis 2 that divorce is an adaptive strategy, we developed a GLMM framework because the detection probability of breeding individuals was close to one (Barbraud & Weimerskirch, 2012). Models were analyzed in R (Team, 2018) using the *lme4* package (Bates et al., 2015). Estimates of parameters and relationships were calculated from an average model of the top model set. The model selection and model averaging on all candidate models are described in Appendix S1: Section S1.4.

Causes of divorce

If divorce is adaptive, then it can be triggered by low breeding success (hypothesis 2a). In this case, divorce can happen either due to a failed breeding attempt at the previous breeding season (short-term breeding success) or lower long-term breeding success averaged during the entire pair bond with the previous partner (long-term breeding success). To test this hypothesis, we modeled divorce and widowhood, which are two mutually exclusive scenarios of a pair-bond disruption, as a binary response variable in a GLMM framework (Equation 1) as

$$Y_{D/W} \sim \text{stBS} + \text{ltBS} + \text{controls} + \varepsilon \quad (1)$$

where $Y_{D/W}$ indicates whether a pair-bond disruption happened through divorce or widowhood; stBS is the short-term breeding success in the previous breeding season before pair-bond disruption; ltBS is the long-term breeding success during the entire pair bond with the previous partner; and ε indicates the year of the pair-bond disruption as a random effect to control for annual variability and environmental disturbance. We also included senescence and pair-bond duration as predictors because they are expected to affect divorce probability (shown as controls in Equation 1). First, we incorporated senescence by including breeding experience, measured as the total number of breeding attempts made by the focal individual until the pair-bond disruption. Since breeding success in wandering albatross increases to a maximum at 17–20 years or 5–7 breeding attempts and then decreases (Weimerskirch, 1992), breeding experience and its quadratic term were both included in the global model to address changes in individual breeding success through lifetime. We used breeding experience instead of age as a predictor because the age of many individuals was unknown, whereas we had precise information on breeding experience for a larger number of individuals. Breeding experience and age are highly correlated (Appendix S1: Figure S5). Second, we included the number of breeding attempts made with the partner to control the effects of pair-bond duration. All continuous variables were scaled (mean = 0 and SD = 1) prior to analysis. A model selection was performed for females and males separately.

Consequences of divorce

As an adaptive strategy, divorce can lead to improved breeding success even with an immediate reduction in breeding success due to the so-called first-year syndrome

(hypothesis 2b). Individuals that changed partners after a divorce may show either a higher annual breeding success (short-term breeding success) or a higher breeding success averaged during the entire pair bond (long-term breeding success) with the new partner compared with the previous partner. However, a temporary cost may obscure signs of improvement in breeding success after divorce as individuals breeding in year t that have previously divorced or lost their partner by death may have lower breeding performance and survival than individuals in a reunited pair (a pair with at least two consecutive reproductions; Naves et al., 2007). In that case, divorce will improve only the long-term breeding success. We did not expect an improvement in breeding success for an individual that changed partners after widowhood.

To assess the change in short-term breeding success after a pair-bond disruption (divorce or widowhood), we performed an analysis in a GLMM framework (Equation 2) as

$$Y_{\text{stBS}} \sim X_{D/W} + b_{\text{exp}} + \varepsilon \tag{2}$$

where Y_{stBS} indicates the difference in short-term breeding success between the breeding performance with the new and previous partner; $X_{D/W}$ represents whether the focal individual changed partners through divorce or widowhood; and ε is the year of the breeding attempt as a random effect to control for annual variability and environmental disturbance. We also controlled for senescence using breeding experience and its quadratic term, b_{exp}.

To assess the change in long-term breeding success after a pair-bond disruption, we performed an analysis in a generalized linear model (GLM) (Equation 3) as

$$Y_{\text{ltBS}} \sim X_{D/W} + \text{nbreed}_{\text{new}} + \text{nbreed}_{\text{pre}} \tag{3}$$

where Y_{ltBS} is the difference in long-term breeding success between the breeding performance averaged within the duration of the pair bond with the new and previous partner; and $X_{D/W}$ represents whether the focal individual changed partners through divorce or widowhood. The numbers of breeding attempts made with the new and previous partners were included in the model to account for effect of pair-bond duration shown as $\text{nbreed}_{\text{new}}$ and $\text{nbreed}_{\text{pre}}$.

Life-history outcomes

To analyze the impacts of pair-bond disruption on life-history outcomes and state occupancy times, an AMC framework was used to calculate the lifetime history outcomes: life expectancy, mean LRS, expected breeding interval, probability of future divorce, and expected time to divorce, depending on individual states (Caswell, 2009; Keyfitz & Caswell, 2005; Roth & Caswell, 2018). In the AMC framework, a finite-state, discrete-time, absorbing Markov chain P (Equation 4) describes the fate of an individual evolving through a set of transient states and eventually being absorbed by a death state. The matrix P contains a transient transition matrix U that describes transitions among transient (living) states and a row vector M that contains probabilities of transition from transient states to the absorbing state (death) (Caswell, 2009, 2011; Roth & Caswell, 2018). The life cycle of wandering albatrosses (section "Life cycle" and Figure 2) corresponds to the transient matrix U. The row vector M contains the death probabilities of individuals at each transient state. Transition probabilities in P are estimated using MECMR models from the section "Capture–mark–recapture model to estimate pair-bond disruption and vital rates."

$$\mathbf{P} = \begin{pmatrix} \mathbf{U} & \mathbf{0} \\ \mathbf{M} & \mathbf{1} \end{pmatrix} \tag{4}$$

The calculations of life expectancy, LRS, breeding intervals, probability of future divorce, and expected time to divorce rely on the fundamental matrix N (Equation 5) derived from U in our stochastic matrix P (Caswell, 2009, 2011, Roth & Caswell, 2018).

$$\mathbf{N} = (\mathbf{I} - \mathbf{U})^{-1} \tag{5}$$

The (i, j) entry in matrix N is the expected time for an individual starting from state j to spend in state i during its remaining lifetime.

The life expectancy is the expected value of remaining longevity (denoted by $E(\eta_j)$), given that the individual is in state j, and is obtained by summing column j of N (Caswell, 2009). For example, the remaining life expectancy for an individual in state S indicates that this individual in a long-term pair bond will live for an additional $E(\eta_{\mathbf{S}})$ years on average.

We calculated expected LRS of an individual currently in state j (denoted by $E(\rho_j)$) by considering reproduction as a reward that is accumulated each time an individual enters a breeding state using methods developed in Caswell (2011) (detailed methods are provided in Appendix S1: Section S1.6.1 and S1.6.2; see also van Daalen & Caswell [2017] for further developments of this method). Specifically, an individual produces an offspring each time it enters a breeding state, with a probability given by the mean breeding success in that state. The values of breeding success probability used in our AMC framework were estimated in the section "Estimates of breeding success." This reproductive reward accumulates

over the remaining lifetime of the individual starting from its current state and ends at the time of death. For example, the remaining LRS for state S means that individuals in a long-term pair bond will produce $E(\rho_S)$ offspring on average.

We calculated the expected time required for an individual to reach its next breeding attempt and the next divorce event depending on its current state. To do this, we considered breeding and divorce as target states for an individual to reach. These target breeding states or divorce states become a new set of absorbing states, along with the death state. The method involves calculating the mean of the time required to reach the new absorbing state, conditional on the individual actually reaching that state. Following the approach described in Roth and Caswell (2018) in the Section 3.2 and 6.2, we rearranged the entries in matrix P to generate a new transient transition matrix U with breeding or divorce states as a set of absorbing target states. The expected time for an individual to breed or divorce again depends on its current state and can be calculated using a newly generated stochastic matrix P in terms of expected time to reach or return to the target set (see Appendix S1: Section S1. 6.3 for detailed methods and examples).

We calculated the probability that an individual will experience a future divorce event, which is the probability that an individual will reach the target divorce states given its current pair-bond status. We used the methods developed in Roth and Caswell (2018) in the sections "3.1 and 6.1 (See Appendix S1: Section S1.6.3 for detailed methods and examples).

The confidence intervals of estimates calculated from the AMC framework were generated by bootstrapping from each MECMR estimate sampled within a normal distribution on a logit scale. The average values between states were weighted corresponding to the relative abundance in the population (Appendix S1: Section S1.6.2).

RESULTS

Pair-bond disruption rates

For both sexes, the probabilities of pair-bond disruption changed over the study period and varied by pair-bond status (see Appendix S1: Figures S7 and S9 for time-varying estimates of widowhood and divorce rates; a time series for the number of divorce and widowhood cases in this population is also present in Appendix S1: Section S2.6).

As expected in hypothesis 1a (Table 1), males had a higher probability of becoming widowed than females (Figure 3a, males: 0.063, standard error [SE] = 0.003 and females: 0.046, SE = 0.004) in this population with higher female mortality rate. Divorce rates differed among all pair-bond status for both sexes. As expected from hypothesis 1b (Table 1), females had an overall higher divorce rate than males regardless of pair-bond status (Figure 3b). As for long-term divorce patterns analyzed by the AMC framework, females had a higher probability of divorcing again in the future (Figure 3c), and their expected time to the next divorce was shorter than that of males (Figure 3d).

Our results characterized a repeatable divorce pattern because (1) individuals breeding with a new partner after a divorce in year $t-1$ (ND) had the highest divorce rate in year t (females: 0.673, SE = 0.030; males: 0.597, SE = 0.044); (2) individuals bonded with a new partner after divorce had the highest probability of eventually divorcing again in the future (Figure 3c, females: 0.655, SE <0.001; males: 0.618, SE <0.001); and (3) individuals bonded with a new partner after divorce had the shortest expected time to divorce again (Figure 3d, females: 4.254, SE = 0.002; males: 5.256, SE = 0.002). Although changes in partner also happened in individuals breeding with a new partner after widowhood (NW) in year $t-1$, their immediate divorce rate (Figure 3b, females: 0.302, SE = 0.056; males: 0.250, SE = 0.051) in year t and the long-term probability of divorcing again in the future (Figure 3c, females: 0.600, SE <0.001; males: 0.575, SE <0.001) were lower than that of ND individuals.

Individuals staying with the same partner in year $t-1$ had the lowest divorce probability in year t (Figure 3b, females: 0.156, SE = 0.015; males: 0.095, SE = 0.011) and were less likely to divorce in the future (Figure 3c, females: 0.502, SE <0.001 and males: 0.470, SE <0.001). Post breeders in year $t-1$ after breeding with the same previous partner (Post-S) also had a lower divorce rate in year t compared with post breeders after breeding with a new partner (Post-N).

Fishing effort and widowhood

Contrary to our expectation in hypothesis 1c (Table 1), no significant relationship between fishing effort and survival or widowhood probability was detected in either females or males (Table 4). Fishing effort in foraging grounds of females and males only explained a small proportion of variation in survival for females and males, respectively (Table 4, female: slope with fishing effort in breeding foraging grounds 0.513, SE = 0.511, in nonbreeding foraging grounds 0.480, SE = 0.510; male: slope with fishing effort in breeding foraging grounds 0.514, SE = 0.511, in nonbreeding foraging grounds 0.516, SE = 0.510). Fishing effort occurring at the foraging grounds of an individual's partner was not associated with the widowhood probability of the focal individual (Table 4, female: slope with fishing effort in breeding foraging grounds 0.534, SE = 0.511, in nonbreeding foraging grounds 0.473, SE = 0.6354; male: slope with fishing

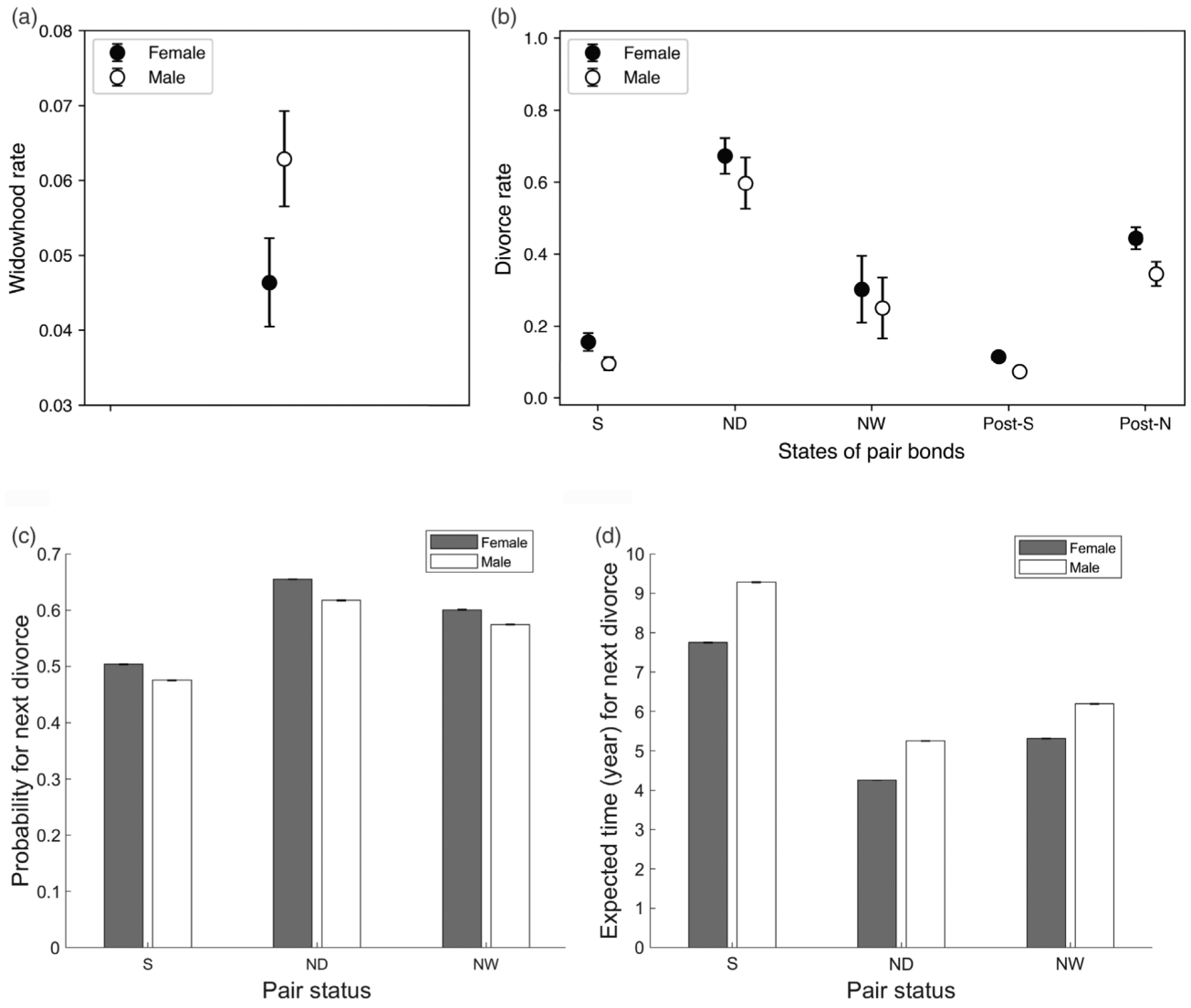

FIGURE 3 Estimates of pair-bond disruption rates from the best supported multievent capture–mark–recapture (MECMR) model and long-term divorce patterns analyzed by absorbing Markov chain (AMC) framework. (a) Probabilities of becoming widowed as a function of sex (±90% confidence interval [CI]), (b) divorce rates as a function of pair-bond status (±90% CI), (c) probabilities of ending current pair bond by divorce in future (±95% CI), and (d) expected time to reach next divorce event depending on current pair-bond status (±95% CI)

effort in breeding foraging grounds 0.507, SE = 0.511, in nonbreeding foraging grounds 0.509, SE = 0.511).

Causes and consequences of divorce

First, we characterized whether divorce was triggered by lower breeding success in hypothesis 2a (Table 1). The effects of both short-term and long-term breeding success with a partner on divorce were included (see Appendix S1: Table S6 and Figure S11 for a list of models and associated results). Contrary to our expectations, females of higher short- and long-term breeding success with a partner had a higher divorce probability (Appendix S1: Section S2.3 and Figure S11), whereas males' divorce probability was not affected by breeding success with a partner (Appendix S1: Table S6).

For both females and males, divorce probability was influenced by pair-bond duration and decreased as the number of breeding attempts with that partner increased (Figure 4a). Breeding experience was also associated with divorce probability (Figure 4b) for both females and males. In females, a quadratic relationship was found, and the probability of divorce was highest for experienced females (~8–10 breeding experiences) and declined from this peak for more experienced females. In males, divorce probability increased linearly with breeding experience, suggesting that older males are more likely to divorce (Figure 4b).

TABLE 4 Results from the ANODEV statistics used to test the effects of fishing effort on survival and widowhood of wandering albatrosses at Possession Island from 1967 to 2011

Sex	Model	Survival	Widowhood	Breed	Divorce	Detection	Np	QAIC	Deviance	Cd (%dev)	*p*-value
Female	1	States	–	–	–	–	294	45625.338	45037.338	...	...
	2	States + t	–	–	–	–	336	45637.958	44965.958	...	...
	3	States + fishery$_f$	–	–	–	–	296	45624.645	45032.645	0.066	0.285
	4	–	States	–	–	–	290	45636.35	45056.35	...	...
	5	–	States + t	–	–	–	332	45614.266	44950.266	...	...
	6	–	States + fishery$_m$	–	–	–	292	45629.795	45045.795	0.099	0.193
Male	1	States	–	–	–	–	309	56605.990	55987.990	...	...
	2	States + t	–	–	–	–	355	56616.642	55906.642	...	...
	3	States + fishery$_m$	–	–	–	–	311	55982.976	56604.976	0.062	0.302
	4	–	States	–	–	–	305	56597.217	55987.217	...	...
	5	–	States + t	–	–	–	347	56615.265	55921.265	...	...
	6	–	States + fishery$_f$	–	–	–	307	56599.886	55985.886	0.020	0.676

Notes: Starting from our supported model with lowest Akaike information criterion corrected by over dispersion (QAIC), we ran tests on survival and widowhood alternatively while keeping the model structure in other demographic parameters from the lowest QAIC model. States indicates that parameters are constrained to be constant but vary among pair-bond status. "+" indicates that the effects on previous pair-bond status is additive (same slope). States + t indicates that parameters are unconstrained and have time variation with same slopes. States + fishery$_{f/m}$ indicates that parameters are constrained as a function of a fishing effort and vary among pair-bond status with the same slope. fishery$_f$ indicates fishing effort on female foraging grounds (nonbreeding and breeding foraging grounds). fishery$_m$ indicates fishing effort on male foraging grounds (nonbreeding and breeding foraging grounds). "Np" indicates number of parameters. "Cd (%dev)" represents the percentage of deviance explained by a given covariate or set of covariates. "–" indicates that the model structure is the same as the model with lowest QAIC.

Second, we characterized the consequences of divorce by analyzing whether a divorce resulted in an improvement in either short-term or long-term breeding success in hypothesis 2b (Table 1). No significant changes in short-term or long-term average breeding success were detected.

Impacts of pair-bond disruption on vital rates

For both sexes, the vital rates changed over the study period and varied by pair-bond status (see Appendix S1: Figures S6 and S8 for time-varied estimates of survival and breeding probabilities).

As expected in hypothesis 3a (Table 1), survival rates differed between individuals breeding with the previous partner (S and Post-S), individuals after a partner change (ND, NW and Post-N), and divorced (D) and widowed (W) individuals (shown in Figure 5a). Individuals staying with the same partner had higher survival rates (female: 0.932, SE = 0.003; male: 0.944, SE = 0.003) than individuals changing partners (female: 0.920, SE = 0.005; male: 0.930, SE = 0.005, Figure 5a). However, these confidence intervals overlapped, so there is a low confidence that these estimates differ.

For mated individuals within a pair bond in year $t-1$ (staying either with the same previous partner or a new partner after a partner change), females had lower survival rates than males, but the opposite pattern emerged for divorced and widowed individuals: divorced and widowed females had higher survival rates (0.977, SE = 0.005) than females in a pair-bond relationship. The survival rates of divorced and widowed males (0.943, SE = 0.004) was similar to males in a pair-bond relationship (staying with the same partner: 0.944, SE = 0.003; with a different partner: 0.930, SE = 0.005) (Figure 5a).

As shown in hypothesis 3a (Table 1), we estimated the breeding probability in year t and showed that breeding probability varied among all pair-bond status in year $t-1$ (Figure 5b). Females had higher breeding probabilities than males for all pair-bond status. Postbreeders (Post-S and Post-N) from year $t-1$ had higher breeding probabilities in year t compared with other states, as expected for a biennial species. For widowed individuals, females had higher breeding probabilities than males (female: 0.320, SE = 0.13; male: 0.184, SE = 0.008).

As for breeding success depending on pair-bond status in hypothesis 3a (Table 1), no significant difference was shown among individuals breeding with the same partner (S, female: 0.812, SE = 0.014; male: 0.819,

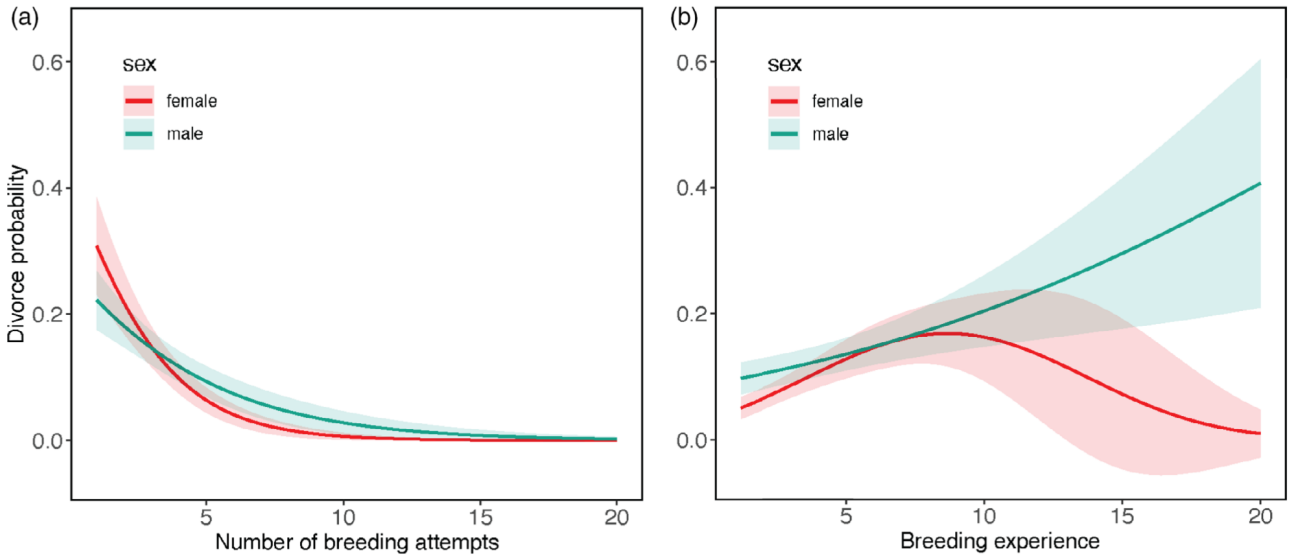

FIGURE 4 Relationships between divorce probability and (a) number of breeding attempts made with a partner (±90% confidence interval [CI]) and (b) breeding experience (±90% CI), in both females and males

SE = 0.012), individuals breeding with a new partner after divorce (ND, female: 0.849, SE = 0.040; male: 0.843, SE = 0.027), and individuals breeding with a new partner after widowhood (NW, female: 0.856, SE = 0.030; male: 0.800, SE = 0.036) in year *t* (Appendix S1: Figure S13).

Impacts of pair-bond disruption on life-history outcomes

As expected in hypothesis 3b (Table 1), we found a reduction in remaining LRS for divorced and widowed males (Figure 6a). Females had a higher remaining LRS than males regardless of their pair-bond status. The remaining LRS of divorced (5.794, SE = 0.004) and widowed (6.031, SE = 0.003) females was no different from that of females within a pair bond (5.841, SE = 0.003). However, the remaining LRS of divorced (4.729, SE = 0.003) and widowed (4.653, SE = 0.003) males was lower than males in a pair bond (5.674, SE = 0.003), with a difference of 16.7% and 18.0% LRS, respectively.

The reduction of the remaining LRS was a result of the extended remating process required by divorced and widowed individuals (Figure 6b). Females had an overall shorter expected time to their next breeding attempt than males. Individuals within a pair bond had much shorter expected time to breed again (Figure 6b, females: 1.911, SE < 0.001; males: 1.911, SE < 0.001) compared to divorced and widowed individuals (Figure 6b, females: 3.270, SE = 0.002; males: 4.346, SE = 0.001). Moreover, widowed and divorced males required 32.9% more time to find a new mate than did females.

Contrary to our expectation in hypothesis 3b (Table 1), no reduction in remaining life expectancy was found in individuals experiencing pair-bond disruption (ND, NW, Post-N, D, and W) compared with individuals staying with the same partner (S and Post-S), as shown in Appendix S1: Figure S10. Female remaining life expectancies depending on their current pair-bond status were as follows: S: 14.970, SE = 0.005; ND: 14.507, SE = 0.006; NW: 14.585, SE = 0.006; Post-S: 14.911, SE = 0.005; Post-N: 14.571, SE = 0.006; D: 17.593, SE = 0.008; and W: 16.536, SE = 0.006. Male remaining life expectancies depending on their current pair-bond status were as follows: S: 17.261, SE = 0.006; ND: 16.703, SE = 0.006; NW: 16.734, SE = 0.006; Post-S: 17.265, SE = 0.006; Post-N: 16.854, SE = 0.006; D: 16.955, SE = 0.007; and W: 16.980, SE = 0.007. Females in a breeding stage (S, ND, and NW) and sabbatical year after a breeding attempt (Post-S and Post-N) had a lower life expectancy than males. Non-breeding divorced and widowed females had a higher life expectancy than females in other states, while males showed no significant difference in life expectancy among states.

DISCUSSION

In this male-skewed population (Weimerskirch et al., 2005), we showed that pair-bond disruption arose from different processes and led to divergent consequences for females and males. As expected, males were more likely to become widowed than females because breeding females had higher mortality rates (hypothesis 1a in Table 1, Figure 3a). Females had a

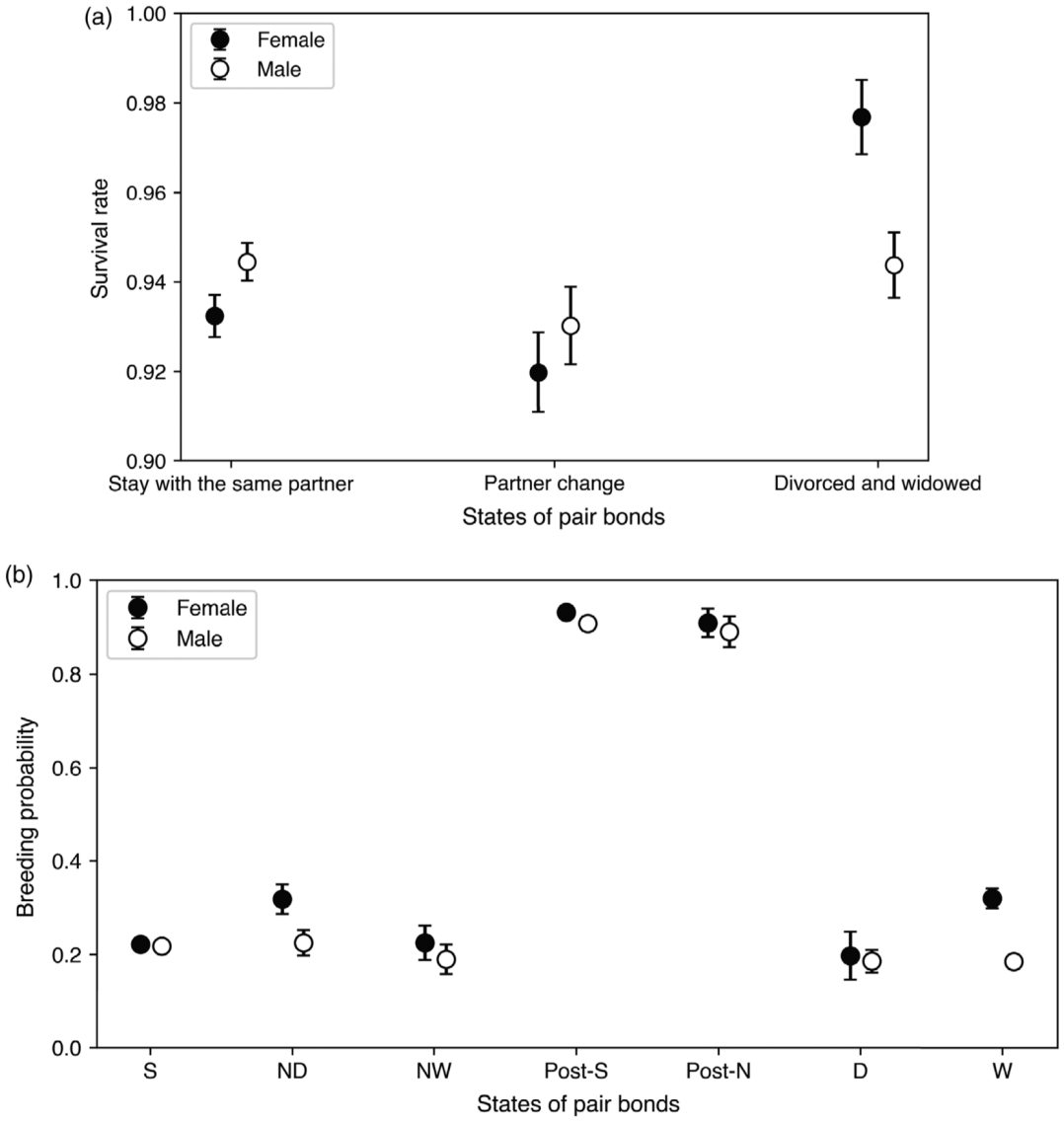

FIGURE 5 Estimates of vital rates (±90% confidence interval [CI]). (a) Adult survival rates depend on pair-bond status. The state "stay with the same partner" includes both breeders and postbreeders in year $t - 1$ that stay with the same partner (S and Post-S). The state "partner change" indicates breeders and postbreeders after breeding with a new partner in year $t - 1$ (ND, NW, and Post-N). The state "divorced and widowed" includes divorced (D) and widowe (W) individuals not bonded with a partner in year $t - 1$. (b) Breeding probabilities depend on current states

higher divorce rate than males (hypothesis 1b in Table 1, Figure 3b), and we propose that divorce is caused by an intruder that displaces a member of the same sex, referred to as the forced divorce hypothesis. Contrary to our expectation (hypothesis 2 in Table 1), divorce does not seem to be an adaptive process in wandering albatross because there was no improvement in breeding success following divorce, even when the effects of the first breeding attempt were accounted for, and poor breeding success had no impact on divorce probability (Appendix S1: Section S2.3). Although there was no detectable impact of pair-bond disruption on annual survival or reproduction in the following year (hypothesis 3a in Table 1), LRS was reduced for males that missed several breeding seasons in this male-skewed population (hypothesis 3b in Table 1 and Figure 6).

Male-biased widowhood rates

As expected, the lower survival rates of breeding females led to a higher probability that males would become widowed in this population of wandering albatrosses (hypothesis 1a in Table 1, Figures 5a and 3a). Breeding females in a pair-bond relationship had lower survival rates

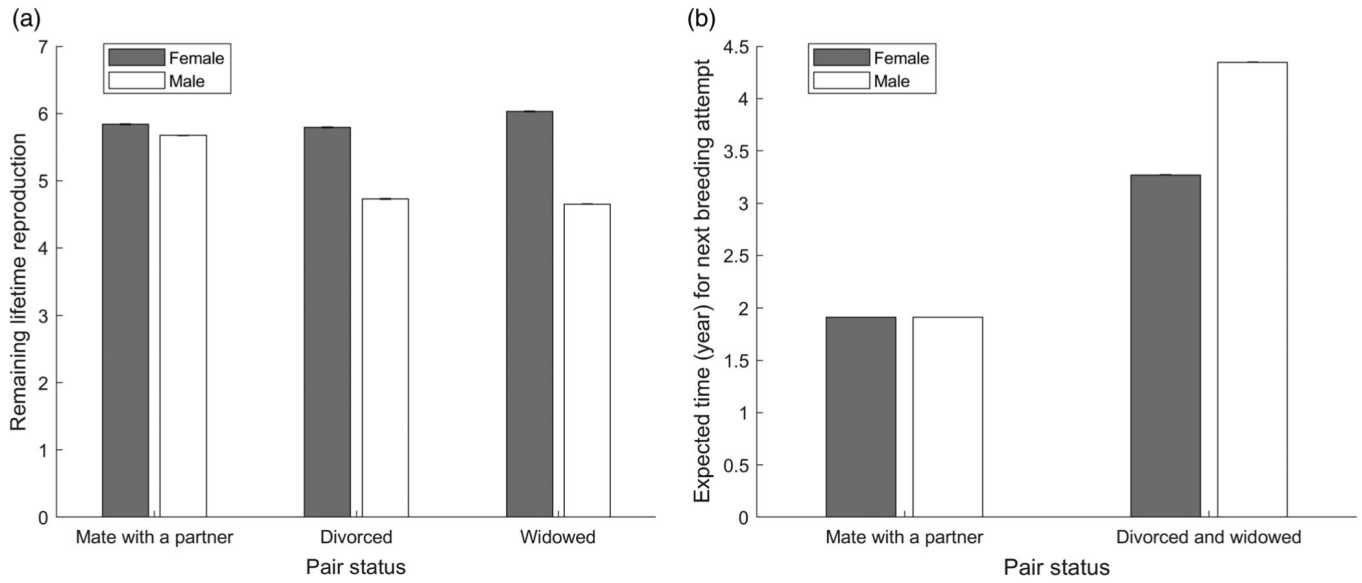

FIGURE 6 Impacts of pair-bond disruption on long-term individual reproductive outcomes (±90% confidence interval [CI]): (a) remaining lifetime reproductive success depending on pair-bond status and (b) expected time to reach next breeding attempt

than males, but the opposite pattern emerged for divorced and widowed females because they had higher survival rates than males (Figure 5a). This pattern suggests a stronger tradeoff between survival and reproduction in females than that of males (Barbraud & Weimerskirch, 2012) since associated costs of reproduction can be higher in females than in males (Weimerskirch et al., 2000). Prey availability is lower for females exploiting subtropical waters, leading to lower prey capture rates than among males foraging in Antarctic and sub-Antarctic waters (Weimerskirch, 1995). Therefore, females must overcome greater difficulties than males while provisioning their chicks (Weimerskirch et al., 2000), which may explain the higher mortality rates of breeding and postbreeding females and, thus, higher widowhood rates of males.

In addition to differences in costs of reproduction and life-history traits between sexes, widowhood can also arise from fishery bycatch mortality (Gianuca et al., 2017; Mills & Ryan, 2005). Contrary to our expectation (hypothesis 1c in Table 1), we did not detect significant impacts of bycatch mortality on wandering albatross survival and widowhood probabilities (Table 4). Our study covered the period from 1967 to 2011, within which fishing effort and population size presented large spatiotemporal variations (Appendix S1: Figure S4). The number of breeding pairs of wandering albatrosses on Possession Island was relatively stable during the 1960s, then a marked decline occurred between the early 1970s and early 1980s, caused by incidental fishery bycatch, followed by a consistent recovery through the late 1980s and 1990s (Appendix S1: Figure S2). The pelagic long-line effort decreased and changed its spatial distribution farther from Possession Island (Weimerskirch et al., 1997), and mitigating measures have been implemented, possibly allowing for a population recovery since the mid-1980s (Barbraud et al., 2013; Weimerskirch, 2018).

In our study, a linear relationship between fishing effort, bycatch mortality, and widowhood was assumed to permit the estimation of identifiable parameters in the MECMR framework. Although this assumption was likely true during the first half of the study period, the implementation of mitigation measures alleviating bycatch rates probably made this hypothesis less likely during the latter duration of the study. Hence, nonlinear approaches may be necessary to comprehend the complexity of spatiotemporal dynamics of long-line fishing effort, changes in fishing practices, and implementation of mitigation measures, but they require larger data sets to obtain identifiable parameters within our complex pair-bond framework. Nonetheless, the fishing effort used in this study was based on the reported fishing effort, which likely underestimated the actual fishery intensity in oceanic waters where females forage owing to the existence of illegal, unreported, and unregulated (IUU) fishing (Weimerskirch et al., 2020). Additionally, a proportion of wandering albatrosses may be more susceptible to incidental mortality from fishing vessels (Barbraud et al., 2013; Tuck et al., 2015). Consequently, the selective disappearance of individuals that are more likely to interact with fishing vessels can also be a factor explaining the absence of a relationship between fishery and widowhood in our results.

Different causes of divorce in females and males

Many studies have shown that divorce may be adaptive (Culina, Lachish, & Sheldon, 2015), including in albatross species (Ventura et al., 2021). However, as Jeschke et al. (2007) pointed out, "adaptive divorce may in general be less common than usually assumed," and a diversity of divorce mechanisms may exist within a population. In wandering albatrosses, we found no support for the adaptive hypothesis but more evidence for a nonadaptive divorce mechanism: the forced divorce hypothesis (Choudhury, 1995), whereby individuals lose their partner as a result of an intrusion from a competitor.

We show that neither lower long-term breeding success with a partner nor the failure of a single breeding attempt increased divorce probability of a pair bond (contrary to hypothesis 2 in Table 1) (Appendix S1: Section-S2.3). In addition, even when the effect of immediate breeding cost of a newly formed pair was excluded, divorce did not yield improvements in long-term breeding success. Hence, the absence of a correlation between breeding success and probability of divorce suggests that divorce is nonadaptive.

Interestingly, we found that divorced individuals tended to divorce again (Figure 3b–d). This repeatable divorce pattern is often nonadaptive because multiple mating in avian species can be costly. Indeed, newly formed pairs have been shown to suffer higher reproductive costs with delayed breeding, lower breeding success, and reduced clutch mass during their first breeding attempt. This has been observed in kittiwakes (*Rissa tridactyla*), blue-footed boobies (*Sula nebouxii*), and wandering albatross populations in South Georgia (Crino et al., 2017; Naves et al., 2007; Sánchez-Macouzet et al., 2014; Weimerskirch, 1992). This repeatable divorce pattern indicates a within-population diversity of divorce mechanisms.

Several nonadaptive divorce hypotheses have been proposed, such as (1) chance event (e.g., arrival assynchrony) or (2) the so-called forced divorce hypothesis (Choudhury, 1995). The first nonadaptive hypothesis assumes that partners may accidentally lose contact due to random perturbations (Black, 1996; Choudhury, 1995). Wandering albatrosses have a quasi-biennial breeding strategy, so the arrival asynchrony of partners, perhaps due to stochastic environmental disturbances at the different nonbreeding foraging grounds, may lead to divorce. However, permanent divorce caused by arrival asynchrony is unlikely because albatrosses have elaborate and long courtship displays and take several years to establish a pair bond (Figure 6b). Notably, some females divorce "temporarily" to breed annually with different males while their long-term partners recover at sea during their sabbatical year (Barbraud & Weimerskirch, 2012; Weimerskirch et al., 2015). Specifically, some females do not take a sabbatical year following a breeding attempt while their long-term male partners do. Hence, in the next breeding season, these females that remain at the colony will breed with a temporary partner. However, they will mate again with their long-term partner when they return from their sabbatical year, so they only have a "temporary divorce." This suggests that permanent divorce is unlikely to be driven by arrival asynchrony or a missing breeding season, and pair-bond disruptions among albatrosses are more likely due to the death of a partner or by an intruder outcompeting one of the partners.

Most divorce events in this population may happen due to a male intruder, potentially younger, that outcompetes the previous male partner in a pair of wandering albatrosses rather than chance events. Here, the increasing rate of divorce in males as aging occurs (measured as breeding experience on Figure 4b) suggests a response to the loss of competitive advantages of older males. Particularly, in this male-skewed wandering albatross population, single males available to mate often interfere with the display courtship processes of formed pairs (personal observations by Henri Weimerskirch). In the southern Georgia population, more males display to females than females to males at each breeding season (Pickering, 1989), and male intrusion should be common during courtship among wandering albatrosses (Pickering, 1989; Weimerskirch et al., 2005; Weir et al., 2011). Perhaps male intruders interfere preferentially in pairs with high-quality females, leading to the higher divorce rates of females with higher breeding success (Appendix S1: Table S6 and Figure S11). However, whether mate choice decisions of male intruders rely on the assessment of female quality according to relative behavioral traits is an open question and will require documentation of the precise behavioral sequences that lead to divorce. For example, mate choice decisions are likely based on behavioral traits such as acoustic courtship displays in great tit (*Parus major*) because singing activity is correlated with exploratory behaviors that can indirectly predict the ability to find food (Munson et al., 2020; Naguib et al., 2010). More research is needed to understand whether male wandering albatrosses choose their female partners with attributes that signal a high probability of successively raising high-quality offspring.

Despite the fact that females are the choosy sex in many species (Ventura et al., 2021), they have never been observed seeking extrapair copulations in this population (Jouventin et al., 2007). Hence, without

information on the precise behavioral sequences that lead to divorce, it is difficult to conclude whether or not females choose to divorce because they are not limited by the availability of mates.

Whether divorce is adaptive in this population of wandering albatrosses requires cautious interpretation. Here, when analyzing the adaptivity of divorce, we focused on breeding success (i.e., fledging success) and tested whether divorce was triggered by a lower breeding success or led to an improvement in breeding success (hypothesis 2 in Table 1). However, an increased divorce rate after a successful breeding attempt does not necessarily demonstrate that divorce is nonadaptive. Divorce after a successful reproduction has been shown to be an adaptive strategy to maximize LRS in multiple plover species (Halimubieke et al., 2019, 2020) or inbreeding avoidance in long-tailed tits (*Aegithalos caudatus*) (Hatchwell et al., 2000). We also found that the divorce probability increases when females have a higher breeding success with their previous partner (Appendix S1: Figure S11). This suggests that females with consistently high breeding success may have higher risk tolerance and rely less on the quality of their male partners for raising offspring and, hence, are less likely to resist takeover attempts. Thus, the higher divorce rate may be a reproductive strategy of high-quality females to breed with diverse partners throughout their life and maximize the number of offspring eventually recruited to the colony. This is also supported by the temporary divorce strategy, which occurs only in females. In our study, individuals with temporary divorce records were removed from our demographic data sets, but this pattern suggests that some females tend to spread their reproductive attempts across several partners. In particular, some females may breed with several partners using temporary divorce, whereas others use definitive divorce, while males are likely forced into divorce. Nonetheless, because wandering albatrosses spend several years at sea between fledging and their first recruitment (Tickell, 1968), the long-term consequences of female divorce in terms of number of offspring recruited to the colony were not assessed in our study. Thus, it is still premature to exclude the possibility that high-quality females use divorce as an adaptive strategy to maximize the number of high-quality offspring recruited to the colony with diverse male partners throughout their life. Further long-term monitoring of offspring quality and recruitment probability is required to understand whether divorce is adaptive in this population. Documenting behavioral sequences that lead to divorces will also shed light on the diversity of divorce mechanisms highlighted in this study.

Divergent consequences of pair-bond disruption between sexes

Contrary to our expectation, pair-bond disruption had no direct significant impacts on annual adult survival for both sexes in wandering albatrosses (hypothesis 3a in Table 1). Even though remating with a new partner can result in energy costs and reduced time available for reproduction during the present breeding season (Jouventin et al., 1999; Real, 1990), the sabbatical year at sea may enable wandering albatrosses with a biennial breeding strategy to recover from those costs, so that neither survival nor breeding probability was affected by pair-bond disruption.

Even if pair-bond disruption did not affect vital rates in the following year, we found a reduction of LRS linked to pair-bond disruption due to missing reproductions (hypothesis 3b in Table 1). Specifically, remating appears to be costly only for male wandering albatrosses since remaining LRS was reduced in divorced and widowed males but not females (Figure 6a). A single pair-bond disruption event diminished the remaining LRS of males by about 17% due to extended remating processes, which can happen each time remating occurs. Within the population, males available to mate were consistently older on average compared to females (Appendix S1: Figure S12). In wandering albatrosses, young individuals remate faster than old ones, and widowed birds tend to mate with other widowed individuals of similar age (Jouventin et al., 1999). As a consequence, older males may have difficulties remating and miss many breeding seasons, while widowed and divorced females have a higher probability of remating because of more mating opportunities in the consecutive breeding season.

Even if divorced and widowed females spend relatively more time breeding again after establishing a new pair bond (Figure 6b), there was no reduction in the remaining LRS of divorced and widowed females compared with females within a pair-bond relationship (Figure 6a). This pattern arises because nonbreeding divorced and widowed females had a higher breeding probability (Figure 5b) because they are the rarer sex and have a longer remaining life expectancy (Appendix S1: Figure S10) and, hence, more reproductive opportunities over their remaining lifetime, which compensates for the number of missed reproduction opportunities following divorce and widowhood.

CONCLUSION

Our study suggests that pair-bond disruption may have a significant cost in LRS, particularly for the abundant sex

in a sex-skewed population. In this population of wandering albatrosses, divorce may not be an adaptive strategy because divorce is independent of past and future reproductive success. However, other characteristics of individual heterogeneity can also play an important role in mate choice and divorce and may obscure signs of an adaptive divorce. For example, in humans, the propensity to divorce is associated with genetically based personality factors (Jerskey et al., 2010; Jocklin et al., 1996). More research is needed to understand the behavioral mechanisms of pair-bond disruptions and their consequences for population dynamics, especially in species experiencing sex-biased demographic rates.

AUTHOR CONTRIBUTIONS

Stephanie Jenouvrier developed the research ideas, conceptualized and designed the study, and led the research activity planning and execution. Ruijiao Sun and Stephanie Jenouvrier developed the MERCM, Ruijiao Sun, Stephanie Jenouvrier, and Hal Caswell developed the AMC models, and Ruijiao Sun and Samantha C. Patrick developed the GLMM. Ruijiao Sun performed all the formal analyses and the results visualization and presentation. Henri Weimerskirch, Christophe Barbraud, and Karine Delord led the curation of the data, prepared the data, and helped interpret the data. Stephanie Jenouvrier and Hal Caswell secured funding. Ruijiao Sun and Stephanie Jenouvrier led the writing of the manuscript. All authors edited and made critical contributions to drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Jenouvrier et al., 2022) are available on the US Antarctic Program Data Center (USAP-DC) repository at https://doi.org/10.15784/601518.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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