

# To breed or not to breed: a seabird's response to extreme climatic events

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**Intermittent breeding is an important life-history strategy that has rarely been quantified in the wild and for which drivers remain unclear. It may be the result of a trade-off between survival and reproduction, with individuals skipping breeding when breeding conditions are below a certain threshold. Heterogeneity in individual quality can also lead to heterogeneity in intermittent breeding. We modelled survival, recruitment and breeding probability of the red-footed booby (*Sula sula*), using a 19 year mark-recapture dataset involving more than 11 000 birds. We showed that skipping breeding was more likely in El-Niño years, correlated with an increase in the local sea surface temperature, supporting the hypothesis that it may be partly an adaptive strategy of birds to face the trade-off between survival and reproduction owing to environmental constraints. We also showed that the age-specific probability of first breeding attempt was synchronized among different age-classes and higher in El-Niño years. This result suggested that pre-breeders may benefit from lowered competition with experienced breeders in years of high skipping probabilities.**

**Keywords:** El Niño; intermittent breeding; age at first breeding attempt; mark-recapture; seabirds; sea surface temperature

## 1. INTRODUCTION

In long-lived species, individuals should be less prone to trade their own survival for that of their offspring, because any reduction in adult survival could greatly reduce lifetime reproductive success [1]. Consequently, long-lived species are believed to respond to environmental constraints by adjusting their breeding effort whereby their own survival should be buffered against environmental variability [2].

In species with a single offspring per breeding season, parents can only regulate breeding effort in the face of environmental constraints by skipping

reproduction for at least one breeding season (hereafter 'skippers'). This strategy of intermittent breeding [3] has been reported in many seabird species. In addition, first-time breeders may have more difficulties than experienced breeders in dealing with environmental constraints [4], such that pre-breeders may decide to delay their first breeding attempt (e.g. recruitment to the breeding population) in some years to avoid high survival costs.

Hence, if birds are able to process predictive information about the quality of the breeding season, they should be aware of a high probability of reproductive failure in some years and preserve their own survival by delaying first breeding or skipping reproduction for breeders [2].

However, non-breeders (pre-breeders and skippers) are difficult to monitor since they generally do not attend breeding colonies, so that estimating the age of first attempted breeding and intermittent breeding requires accounting for detectability less than one and dealing with unobservable individuals. Such studies have quantified intermittent breeding but did not identify correlated environmental mechanisms (e.g. [5]). Individual heterogeneity [6] and density dependence on breeding grounds [7] have been shown to influence recruitment. However, whether the above predicted life-history trade-off plays an important role in regulating age of first breeding attempt and intermittent breeding remains unclear.

We investigated the temporal variation in age at first breeding attempt and the occurrence of intermittent breeding by analysing 19 years of data on individually marked red-footed boobies (*Sula sula*). Using multi-state capture-recapture models incorporating unobservable states, we estimated juvenile and adult survival, age at first breeding attempt and probability of attempting breeding, in adults while accounting for the detection process. We further assessed the effect of the El-Niño Southern Oscillation (ENSO), specifically local mean sea surface temperatures (SSTs), on the age-specific probability of first breeding attempt and on the probability that a breeder decides to skip reproduction for one year.

## 2. MATERIAL AND METHODS

### (a) *Species and study site*

Mark-recapture data were obtained from the capture and banding of red-footed booby chicks and adults on Johnston Atoll (16°45' N, 169°31' W) from 1983 to 2002. The atoll was visited 24–40 days each year between February and July.

Red-footed boobies lay only one egg [8]. All captured adults were breeding birds because pre-breeders and skippers are not present in the colony during the breeding season. We banded chicks between six weeks of age and fledging, and thus our estimates of juvenile survival do not include mortality occurring prior to six weeks of age. Chicks fledge at approximately 14 weeks, depart the atoll 4–12 weeks later and are not observed until their first breeding attempt some years after. Following breeding, adult red-footed boobies depart the atoll, and their location from September to December is unknown.

### (b) *Climate*

El-Niño events at Johnston Atoll are accompanied by reduced up-welling around seamounts where boobies normally feed, and an increase in the SST is generally associated with changes in productivity at lower trophic levels [9]. To determine the extent to which local conditions at Johnston varied, we used local SST anomalies (obtained from the National Oceanic and Atmospheric Administration) as an indicator of environmental fluctuation. Mean SST anomalies were calculated from the four 1° blocks centred at

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16° N, 169° W for the period from January to August during which birds inhabit the atoll.

### (c) Capture–recapture analyses

We analysed 11 357 individual encounter histories using multi-state models [10] implemented in program E-SURGE [11]. We considered four states to represent the different phases of the species life cycle: pre-breeder (PB), breeder (B), skipper (S) and dead individuals (†). Pre-breeders were observed when banded as chicks and were then unobservable until they returned to the colony for their first breeding attempt; skippers and dead individuals were never observed. We estimated pre-breeder and adult survival (breeder and skipper survival are not separately identifiable since skippers are unobservable) and the following transition probabilities: (i) probability of age-specific first breeding attempt (transition from state PB to B, hereafter  $\Psi_1$ ), (ii) probability of entering the skipping state for breeders (transition from state B to S, hereafter  $\Psi_2$ ) and (iii) probability of returning to the colony for skippers (without distinction between 1-year skippers and multiple-year skippers; transition from state S to B, hereafter  $\Psi_3$ ). From (iii) we derived the complementary probability of skipping breeding one more year for skippers (remain in state S; electronic supplementary material, appendix S1). The probability of returning to the colony or being observed at the colony was defined as attempting breeding, not necessarily successful breeding.

We first investigated a general structure for the model [12]. We analysed 32 model combinations in which  $\Psi_1$  was modelled as a constant or quadratic functions of age and time, either singly, additively, or with interactions. We considered 19 age classes, corresponding to the length of the study.  $\Psi_2$ , juvenile survival and breeder recapture probabilities were allowed to be constant or to vary with time. Owing to identifiability issues, we considered models with constant adult survival and constant  $\Psi_3$ . Using a Bayesian approach, we further checked that allowing time variation on these parameters did not affect our estimates (electronic supplementary material, appendix S2). Models were ranked using Akaike's information criterion (AIC, [13]). After identifying time-dependent parameters, we further investigated the effect of SST in describing the time variation by performing an analysis of deviance (ANODEV) and calculated the proportion of variance explained by the covariate using the  $R^2$  statistic [12].

### 3. RESULTS

The best identifiable model showed constant adult survival, time-dependent pre-breeder survival, a quadratic effect of age interacting with time on the probability of first breeding attempt, time-dependent probability of entering the skipping state for breeders, constant probability of returning to the colony for skippers and time-dependent detection probability. All other models were greater than 10 AIC units away (electronic supplementary material, appendix S3).

Annual pre-breeder survival varied between 60 and 100 per cent and adult survival was 90 per cent (table 1). Breeder detection probability ranged from 37 to 99 per cent. The ANODEV showed a significant effect of the local SST anomaly ( $F_{1,17} = 5.9312$ ,  $p = 0.026$ ) on the probability of entering the skipping state for breeders. Nearly 26 per cent of the temporal variation in skipping probabilities was explained by SST variation. High skipping probabilities (figure 1*b*) were synchronized with years of El-Niño events corresponding to peaks in the SST values (figure 1*a*), both in the model in which the probability of skipping breeding was a function of SST values and in the model in which the probability of skipping breeding was allowed to vary freely with time. About 20 per cent of breeders decided to skip reproduction during the 1986–1987 El-Niño event, 15 per cent during the 1991–1994 event and 17 per cent during the 1997–1998 event versus less than 10 per cent in non-El-Niño years.

Table 1. Parameter estimates (with 95% confidence intervals) from the best model. All parameters are reported except for the probability of skipping breeding (figure 1). Arithmetic mean is given for pre-breeder's survival and for breeder's detection probability.

parameter	estimate with 95% CI
mean pre-breeder annual survival	$0.85 \pm 0.0527$
adult annual survival	$0.92 \pm 0.0028$
probability of returning to the colony for skippers	$0.43 \pm 0.0361$
probability of skipping one more year for skippers	$0.56 \pm 0.0361$
mean detection probability for breeders	$0.61 \pm 0.0105$

Age at first breeding attempt was between 2 and 6 years with a probability of about 100 per cent at 7 years (figure 2*a*). Probabilities of first breeding attempt varied similarly with time among the different age classes (figure 2*b*). The ANODEV showed a significant effect of the local SST anomaly ( $F_{2,33} = 5.2774$ ,  $p = 0.010$ ) with nearly 25 per cent of the temporal variance in the probability of first breeding attempt explained by local SST variation, independently of pre-breeder age. El-Niño events were associated with higher probability of first breeding attempts especially in 1987, 1991 and 1997 (figure 2*b*). Another peak was observed in 2000 but was not associated with high SST values.

### 4. DISCUSSION

We provided evidence for a possible effect of environmental conditions on the occurrence of intermittent breeding in a tropical seabird species, the red-footed booby. El-Niño events, through local increased SST values, were associated with high probability of skipped reproduction (figure 1). Previous studies found that intermittent breeding was unrelated to environmental factors but seemed to be rather a consequence of heterogeneity in individual quality (e.g. [5]). On the contrary, our results revealed that intermittent breeding in red-footed boobies was highly influenced by environmental conditions. This suggests that skipping was, at least partly, an adaptive strategy of birds to face the survival–reproduction trade-off, although we expect that heterogeneity among individuals play a role as well, with lower quality individuals being more prone to skip breeding under severe breeding conditions.

Moreover, we showed that the SST anomaly positively influenced the probability of first breeding attempt, independent of age. Higher probabilities of first breeding attempt were associated with years of high SST values, when food supply may be reduced, and also when a large proportion of breeders skipped breeding. This result suggested that the cost of reproduction for first-time breeders could be more influenced by competition with experienced adults than by the quality of the breeding season [7], which was in agreement with the high competition for nest sites observed at Johnston Atoll.

Our results add to the evidence that El-Niño can have deleterious impacts on seabirds (e.g. [14,15])

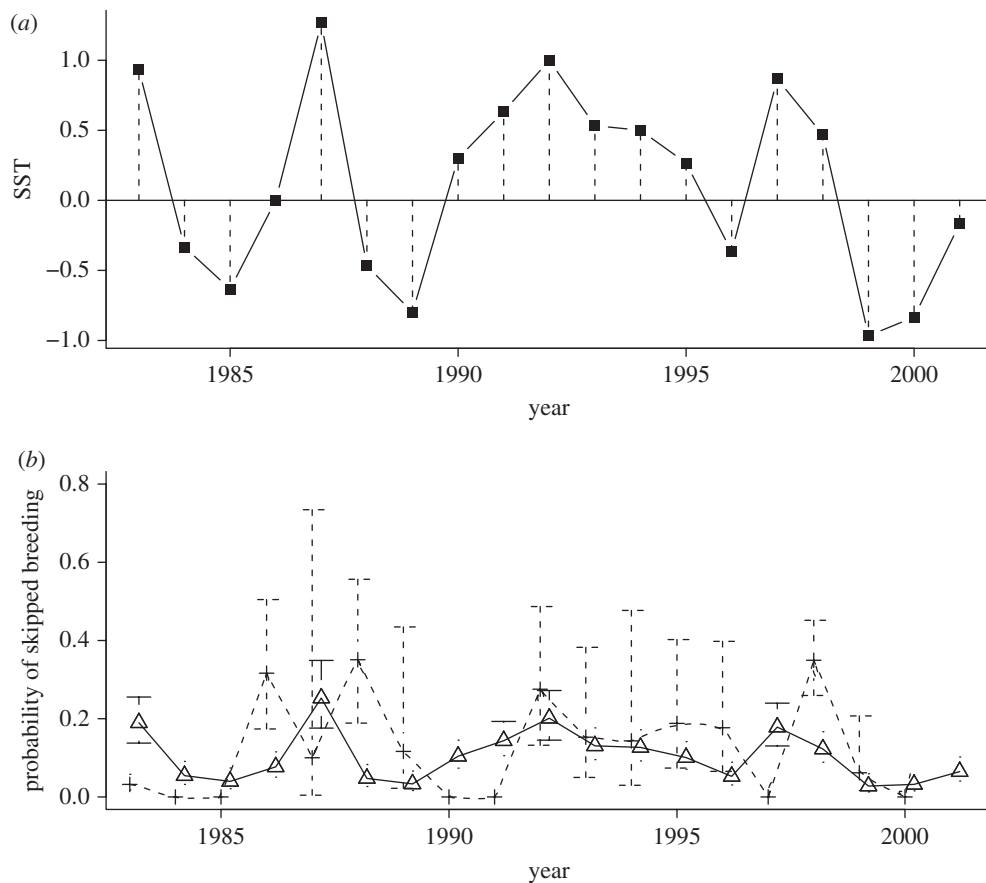


Figure 1. (a) Sea surface temperatures (SSTs) from 1983 to 2002 for the January–August period at Johnston Atoll. (b) Probability of skipped breeding from 1983 to 2002 (with 95% confidence intervals) estimated from the time-dependent model (dashed line) and the covariate model (solid line). For the former, the estimate for the last time interval is not displayed as it is not identifiable.

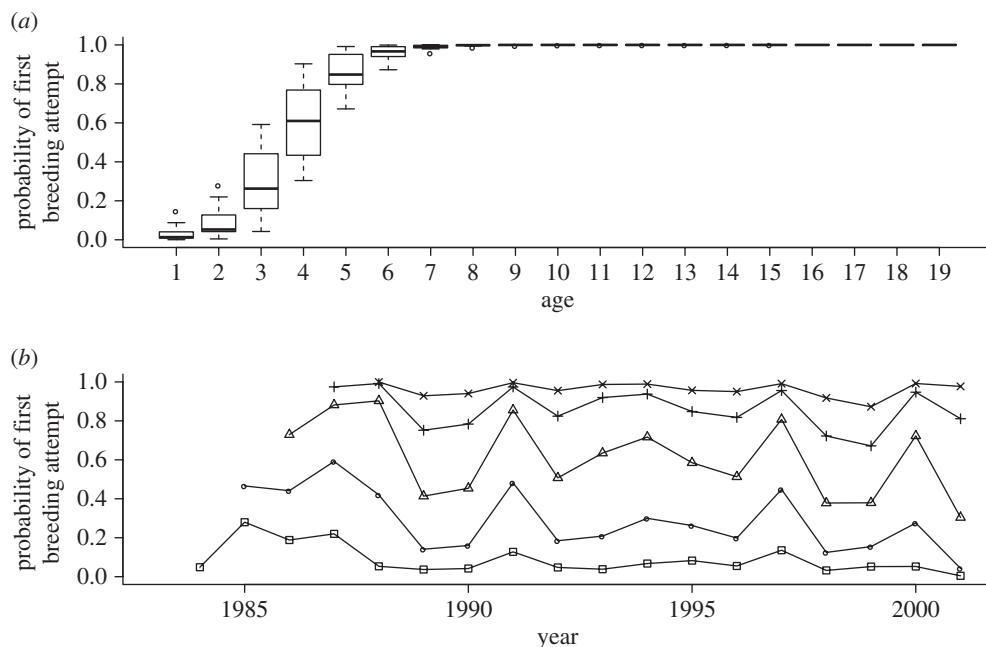


Figure 2. (a) Probability of first breeding attempt (with 95% confidence intervals) as a function of age. Estimates were obtained from the best model. (b) Time variation of the mean probability of first breeding attempt. Squares, 2 year old; circles, 3 year old; triangles, 4 year old; plus, 5 year old; crosses, 6 year old.

and were consistent with studies that reported low numbers of breeding pairs and/or nest counts related with El-Niño events in tropical and Antarctic species

[16,17]. As future scenarios predict more frequent and more intense ENSO events [18], our results indicate that they can affect population dynamics, not only

through immediate consequences but also over consecutive years by modifying intermittent behaviours and recruitment processes.

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