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Testing life history predictions in a long-lived seabird: a population matrix approach with improved parameter estimation

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Life history theory and associated empirical generalizations predict that population growth rate (λ) in long-lived animals should be most sensitive to adult survival; the rates to which λ is most sensitive should be those with the smallest temporal variances; and stochastic environmental events should most affect the rates to which λ is least sensitive. To date, most analyses attempting to examine these predictions have been inadequate, their validity being called into question by problems in estimating parameters, problems in estimating the variability of parameters, and problems in measuring population sensitivities to parameters. We use improved methodologies in these three areas and test these life-history predictions in a population of red-tailed tropicbirds (*Phaethon rubricauda*). We support our first prediction that λ is most sensitive to survival rates. However the support for the second prediction that these rates have the smallest temporal variance was equivocal. Previous support for the second prediction may be an artifact of a high survival estimate near the upper boundary of 1 and not a result of natural selection canalizing variances alone. We did not support our third prediction that effects of environmental stochasticity (El Niño) would most likely be detected in vital rates to which λ was least sensitive and which are thought to have high temporal variances. Comparative data-sets on other seabirds, within and among orders, and in other locations, are needed to understand these environmental effects.

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Understanding the demography of organisms allows us to examine the evolution of their life histories and the strength of selection on various life history traits such as fecundity, age-specific breeding probabilities, and survival. Assessing how such vital rates, and variation in these rates, contribute to population growth has been the focus of recent work (Gaillard et al. 1998, 2000, Pfister 1998) with population matrix models being used to assess the sensitivity of population growth (λ) to differing vital rates (Caswell 2001).

Some generalities from studies using this approach are becoming apparent. In long-lived species with delayed breeding, λ is most sensitive to survival rates, particularly adult survival, and least sensitive to vital rates associated with reproduction (Pfister 1998). These general results have been found in birds (Saether and Bakke 2000), turtles (Heppell 1998) and mammals (Gaillard et al. 1998, 2000, Heppell et al. 2000).

Selection pressures on these vital rates can be predicted by sensitivity analysis (Benton and Grant 1996,

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Caswell 2001). If λ is a good surrogate for fitness, and small changes in a vital rate (such as survival) cause large changes in λ, we can expect natural selection to act most strongly on that particular trait, assuming trade-offs do not exist and that vital rates are independent of each other. Thus we expect proportional sensitivities (also referred to as log-scaled sensitivities or elasticities) to measure selection pressure on particular traits (Benton and Grant 1996, 1999). In addition, traits with high proportional sensitivities may have low variances due to canalization of these traits through stabilizing selection pressure (Stearns and Kawecki 1994). In a review of 30 field populations ranging from a marine alga to terrestrial vertebrates, Pfister (1998) found that the vital rates to which λ was most sensitive were those that were also the least variable. This result was further supported by Gaillard et al. (1998, 2000), who suggested that vital rates to which λ was less sensitive were subject to greater variability and more affected by limiting factors caused by density dependence or environmental stochasticity. A similar argument that more 'behavioral buffering' was associated with survival than reproductive success was made by Cairns (1992) specifically for seabirds.

El Niño-southern oscillation events (Cane 1983) are examples of potentially severe stochastic environmental events that have had pronounced effects on seabird populations around the world (Schreiber and Schreiber 1989, Duffy 1990). Multiple oceanographic and atmospheric features are altered throughout the world during El Niño events which occur approximately every 2–7 years (Cane 1983, Trenberth et al. 1998). In the central Pacific Ocean the thermocline deepens, easterly trade winds are reduced or even reversed, and normal precipitation patterns and normal upwellings change (Wyrtki 1975, Cane 1983, Rasmusson and Wallace 1983). These changes alter the availability of fish to seabirds and thus can affect parameters such as reproductive success, chick growth rates, adult mass, and survival (Schreiber and Schreiber 1984, 1989, Duffy 1990).

We predict that during El Niño events vital rates to which λ is most sensitive, such as adult survival in a long-lived seabird, should be relatively buffered and that any negative changes in vital rates should most likely be seen in rates with low sensitivities, such as those associated with reproduction.

There is mixed support for this prediction. During or shortly following particularly intense El Niño events, colonies of seabirds often have reduced reproductive success, particularly in the Pacific (Schreiber and Schreiber 1984, 1989, Hodder and Graybill 1985, Hatch 1987, Anderson 1989, Boersma 1998). The effect of El Niño on survivorship of seabirds is not as clear, owing to the difficulty of collecting appropriate data for analysis. There is some suggestion that survivorship is reduced, based on evidence of increased numbers of carcasses found washed up on beaches (Bailey and Davenpor 1972, Hatch 1987, Work and Rameyer 1999) and of reduced abundance estimates after El Niño events (Schreiber and Schreiber 1989, Boersma 1998). However these estimates are not based on statistical methods such as mark–recapture analysis (Lebreton et al. 1992, Williams et al. 2002), and interpretation of these data must be made with caution. Using modern mark–recapture analysis techniques Brichetti et al. (2000) found no effect of the warm El Niño period on adult survival of a Mediterranean population of Cory's shearwaters (*Calonectris diomedea*). However they did find an effect of the cold period (La Niña) on survival and attributed this to increased frequency of hurricanes in the Atlantic Ocean. To our knowledge, no study has examined the effects of El Niño events on both fecundity and survival of Pacific seabirds using appropriate estimation techniques.

In this paper, we note three methodological deficiencies affecting much of the work that the above theoretical framework and predictions rest upon. We will address these deficiencies, and attempt to avoid them in our analysis by means of recent methodological advances.

First, log-scaled sensitivities (elasticities), which measure the relative change of λ in response to relative changes of a life history parameter, may not be appropriately scaled, especially in the case where parameters are bounded by 0 and 1 (e.g. survival rates; Link and Doherty 2002). If a population matrix model were parameterized with mortality or with survival (complementary rates), one would expect the corresponding sensitivity metrics to differ only by sign. However this is not the case for elasticities (Olesiuk et al. 1990, Brault and Caswell 1993, Hunter et al. 2000) because the means and variances of the vital rates are not independent and log-scaling does not eliminate the dependence (Link and Doherty 2002). This log scaling may lead to inappropriate conclusions concerning ranking of variables to which λ is most sensitive. A scaling that is more appropriate for such binomial parameters, at least for some purposes, is $\sin^{-1}\sqrt{\theta}$ (Link and Doherty 2002).

As previously stated, a second deficiency in much of the work done to date concerns parameter estimation. Survival is often the most sensitive vital rate, especially in long-lived animals (Pfister 1998). However many survival estimates do not account for probabilities of detection (Saether and Bakke 2000), which can lead to biased estimates of survival, a fact that could lead to the incorporation of poor estimates in matrix models and to misleading results. Similarly, age at maturation has been suggested to be an important vital rate component (Heppell et al. 2000), however estimates of age-specific breeding probabilities corrected for survival and detection probabilities are lacking, leading to estimates that are not valid. Recently, methodologies to remedy this situation have been developed (Clobert et al. 1994,

Pradel and Lebreton 1999, Schwarz and Arnason 2000, Spendelow et al. 2002, Williams et al. 2002, Lebreton et al. 2003).

Lastly, one of the generalizations from the above review papers is that temporal variances in vital rates and their corresponding log-scaled sensitivities are negatively correlated; the rates to which λ is most sensitive are the least variable temporally (Pfister 1998, Heppell et al. 2000, Saether and Bakke 2000). However, in none of these studies is the distinction between biological process variation (the temporal variation in which we are most interested) and sampling variation (variation associated with the estimation process and having nothing to do with the true process variation) distinguished. This problematic feature has been recognized (Gaillard et al. 1998, Saether and Bakke 2000, Wisdom et al. 2000) but not rectified. Recently, methods have been developed to partition variance measures into biological process and sampling variation (Burnham et al. 1987, Skalski and Robson 1992, Link and Nichols 1994, Gould and Nichols 1998). In addition, when correlating sensitivities and estimated variances, both measures need to be scaled appropriately to avoid interpreting mathematical consequences as biologically interesting outcomes (Link and Doherty 2002).

We incorporate the above improvements in scaling sensitivities, parameter estimation, and estimation of variance terms in our study of a long-lived seabird, the red-tailed tropicbird (*Phaethon rubricauda*). Seabirds present an interesting system with respect to life history theory because their life history characteristics are often considered extreme: low fecundity, deferred maturity, and high annual survival. However, there are relatively few long-term data-sets on seabirds, and the contributions of the various demographic characteristics to seabird population growth are little understood. Additionally, owing to the absence of long-term data-sets, we have not been able to fully examine the effect of environmental stochasticity on demographic parameters of seabirds. Our seventeen-year data-set on red-tailed tropicbirds, continuing through several El Niño events, now allows us to assess the contribution of various life stages and vital rates to population growth.

Specifically, we estimate reproductive success from this data-set and, using mark-recapture analyses, estimate survival and age-specific breeding probabilities taking probabilities of detection into account. Using weighted averages of these estimates, we then construct a population matrix model to test the prediction that the sensitivity of λ to survival rates will be greater than to variables associated with reproduction. We then test our second prediction that, properly scaled, biological process variation in vital rates will be negatively correlated with their variance-scaled sensitivities. Lastly, we test the prediction that during environmental events, such as El Niño, vital rates with high sensitivities should be buffered against negative effects. Thus, if we detect negative effects, they should be most evident in vital rates with the lowest sensitivities (i.e. reproductive success).

Material and methods

Study area

Johnston Atoll (16° 45′ N, 169° 31′ W, central Pacific Ocean) is one of the most isolated atolls in the world, located between the Hawaiian Islands and the Marshall Islands. It consists of two entirely man-made islands and two small sand bars that were augmented by extensive dredging, forming a total landmass on the atoll of about 2.6 km^2. Military construction and dredging began in 1939 and the added land mass has allowed the nesting population on the atoll to increase to approximately 500,000 seabirds.

Study species

The red-tailed tropicbird is a tropical, colonially nesting seabird and is highly philopatric, returning to its natal island, and nesting each year in the same site. Tropicbirds exhibit deferred maturity and first begin breeding at a mean of three years of age (Schreiber and Schreiber 1993) with some individuals returning in their first year and most birds first returning by age 6. Individuals may re-mate if a mate does not return one year, but they generally establish a new nest within 150 m of the original nest site (Schreiber 2000). Tropicbirds invariably lay one egg and raise only one chick per year. Approximately 3200 pairs nested on Johnston Atoll in 2000 with the population increasing from 600 pairs in 1984.

Data collection

From 1983 through 1999, two to four visits were made each year to Johnston Atoll, totaling one to two months time per year. Visits early in the year (Jan.–Feb.) were focused on ringing breeding adults. Nests were monitored for reproductive success and on later visits (May–June) chicks were ringed just before fledging. Attempts were made to recapture as many adults as possible each year. In 1986 the U.S. Fish and Wildlife Service stationed personnel on the atoll and they have increased the ringing and recapture efforts. Rings showing wear were replaced and ring loss is unlikely to have occurred.

From 1983 through 1999, 19,357 tropicbirds were ringed as chicks and are thus of known age. An additional 6,467 tropicbirds were ringed as unknown-aged breeding adults. Ringing locations on the atoll by island and ages of birds ringed were recorded (adult or

chick). This and previous studies indicate little to no inter-island movement within Johnston Atoll (< 1% per year), or to other atolls (Schreiber and Schreiber 1993, Schreiber 2000).

Defining El Niño events

All analyses were done with parameters defined in correspondence to a calendar year (Jan.–Dec.), similar to the breeding cycle of the birds. El Niño events, however, do not occur on a calendar year schedule and a determination had to be as to which years to consider El Niño years in the analyses. There is no consensus among oceanographers as to the exact definition of an El Niño. Authors have used differing combinations of southern oscillation index, deepened thermocline in the central and western Pacific, increased sea surface temperature (SST) in the central and western Pacific, and weakened trade winds to indicate the presence of an event (Kiladis and Vanloon 1988, Glantz 1996). All of these criteria vary in intensity and degree during each separate event (Climate Diagnostics Bulletin, published monthly 1982–2000). Trenberth (1997), in an attempt to keep the definition as simple as possible and to match conventional wisdom as to what have been historically considered as events, suggests selecting a single criterion. An El Niño event is considered to be underway when the 5-month running mean SST anomaly in region 3.4 (5°N–5°S, 120°–170°W) exceeds 0.4°C for 6 months or more. In our analyses we considered a year to be an El Niño year if it met the above condition during at least 5 months of a calendar year. For instance, the 1986–87 El Niño continued through Feb. 1988 according to Trenberth's (1997) definition. Given that it only affected 2 months of 1988, we did not consider that year to be an El Niño year in our analyses. According to these criteria the following years were considered to be El Niño years in our analyses: 1983, 1986–87, 1991–94, 1997–98.

Parameter estimation

Since 1992, Fish and Wildlife Service personnel have monitored reproductive success on Johnston Island study plots by checking nests throughout the incubation period. Chicks were ringed between 21 days of age and fledging, and the first year survival estimate began with late-stage (> 20 days) chicks. Overall reproductive success was estimated as the number of fledged chicks from sampled nests divided by the number of sampled nests in which an egg was laid.

We used capture-mark-recapture analyses (Cormack 1964, Jolly 1965, Seber 1965) as modified by Spendelow et al. (2002) and Williams et al. (2002) to estimate adult and juvenile probabilities of recapture and survival as well as age-specific breeding probabilities. Specifically we used the method outlined in Williams et al. (2002) which follows the approach of Clobert et al. (1994). Following Williams et al. (2002) we defined the following threshold ages:

k – the first age at which an animal can breed
m – the age by which all animals breed

and the following model parameters:

p_i^{k+} – the probability that a marked breeder (denoted as age k+) in the study population at sampling period i is captured or observed during period i;
φ_i^{k+} – the probability that a marked animal of age > k survives until period i+1 and remains in the population;
φ_i^0 – the probability that a young animal (age 0) released at sampling period i survives until sampling period i+k;
$\alpha_i^{(v)}$ – the probability of breeding for an animal of age v at sampling period i that has not previously bred.

Following Williams et al. (2002) we made the following assumptions with this modeling parameterization:

1) the age k of first possible breeding is known;
2) all animals become breeders by age m;
3) every young animal released at age 0 in sampling period i has the same probability φ_i^0 of survival until sampling period i+k;
4) every marked animal aged > k in sampling period i, regardless of breeding status, has the same probability φ_i^{k+} of survival until sampling period i+1;
5) every marked breeding animal present in the population at sampling period i has the same probability p_i^{k+} of being recaptured;
6) marked prebreeding animals of age > 0 are not exposed to sampling efforts and have a probability of 0 of being captured in any sampling period;
7) every marked prebreeding animal of age v, where k < v < m, in sampling period i has the same probability $\alpha_i^{(v)}$ of initiating breeding and becoming a breeder in i;
8) every marked animal that attempts to breed for the first time in period i, breeds with probability 1, or with asymptotic adult breeding probability, at all sampling periods after i;
9) marks are not lost;
10) sampling periods are instantaneous and recaptured animals are released immediately;
11) except for the temporary absences of prebreeders, all emigration from the sampled area is permanent;
12) the fate of each animal with respect to capture and survival probability is independent of the fate of other animals.

This method has most recently been used to estimate survival and age-specific breeding probabilities in roseate terns (*Sterna dougallii*, Spendelow et al. 2002, Lebreton et al. 2003). Note that both roseate terns and tropicbirds are island-nesting colonial seabirds with similar life history characteristics. We modeled adult and juvenile survival ($\varphi_i^{(k+)}$and $\varphi_i^{(0)}$) and probability of recapture (p_i^{k+}) as functions of time (i). Although there may be some evidence for further age-specific survival in near-shore seabirds (Nur and Sydeman 1999), we did not feel a priori that this was the case for pelagic tropicbirds.

We did fit models with two types of trap response; a transient parameter (γ) reflecting trap response in survival probability of newly caught breeders and direct trap response (p_i') in capture probability (Williams et al. 2002). The transient parameter estimates the probability of newly banded breeding birds becoming resident (not permanently emigrating) after initial ringing. Including distinct parameters for direct trap response allows for different probabilities of recapture for breeders in time i that were (p_i) and were not (p_i') captured in the previous period, $i-1$. These 'nuisance' parameters may be needed to deal with both temporary and permanent emigration from Johnston Atoll. We modeled γ as a constant and p_i, as well as p_i' as time-varying. We assume that very few birds start breeding at ages 1 and 2, with more birds starting to breeding at ages 3, 4, and 5, and all birds attempting to breed by age 6 ($k=6$). In our experience few birds return for the first time after age of 6 and we simplified our modeling to reflect this. We modeled age-specific breeding probabilities ($\alpha_i^{(v)}$) for ages 1–5 where i is study year and v is age. To further investigate age-specific breeding probabilities, we developed additional models with lower limits on the age of first possible breeding ($v=2$ or 3) and an upper limit of age 4. We used Akaike's Information Criteria corrected for small sample size and overdispersion ($QAIC_c$) to compare and rank models (Burnham and Anderson 2002) that we constructed using program SURVIV (White 1983). Although our best-fit models had time-specificity in survival and age-specific breeding probabilities, in order to obtain time-averaged estimates, we also constructed a model with time-invariant parameters for survival and age-specific breeding probabilities.

Temporal variances of the point estimates obtained using the above approach include both sampling variance (associated with the estimation process and the fact that $p<1$) and biological process variance (true temporal variation in the underlying parameters of interest). To estimate temporal process variation we used methods as formulated by Link and Nichols (1994) and Gould and Nichols (1998). True temporal variability (τ^2) was estimated using Eq. 2 in Gould and Nichols (1998):

$$\tau^2 = S^2 - \frac{1}{n}\sum_{1}^{n}\hat{E}[Var(\hat{\varphi}|F)] + \frac{2}{n(n-1)} \times \sum_{i<j}\hat{E}[Cov(\hat{\varphi}_i, \hat{\varphi}_j|F)]$$

where the first term (S^2) is the estimated total temporal variance of the point estimates, the second term is the average of the time-specific sampling variance estimates and the third term is the average of the time-specific sampling covariance estimates. We used this method to estimate true process variance in the survival and age-specific breeding probabilities. For reproductive success estimates, we assumed no temporal covariance between estimates. Using this approach it is theoretically possible to obtain negative process variance estimates. Since these have no biological meaning we adjust such results to zero. Since we were interested in the relation between sensitivity of λ to different parameters, θ, and variability in θ, on the $\sin^{-1}\sqrt{\theta}$ scale; the delta-method approximation to the variance of $\sin^{-1}\sqrt{\theta}$ is $Var(\theta)/(1-\theta)$.

Population matrix models

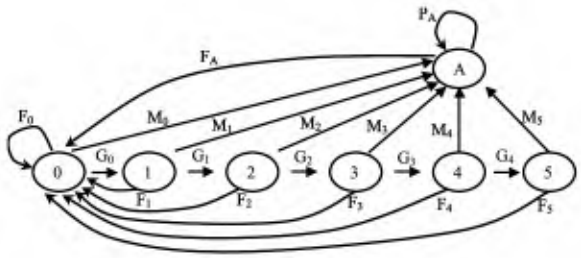
We constructed a stage-based, post-breeding population matrix model (Caswell 2001) using program ULM (Legendre and Clobert 1995) parameterized with averages of reproductive success, as well as survival and age-specific breeding probabilities derived from the capture-mark-recapture analysis. Following our estimation, we constructed a model with seven stages: chicks, 1-, 2-, 3-, 4-, 5-year-old birds and adults (Fig. 1). The model is of the form:

$$n(i+1) = An(i)$$

where n(i) is a vector giving the number of individuals in each stage in the population at time i, and A is a population projection matrix (Caswell 2001). The projection interval (from i to $i+1$) is 1 year. The matrix and the corresponding life cycle diagram are shown in Fig. 1, and formula details for matrix elements and parameter values are given in Table 1. We calculated the asymptotic growth rate (λ) from this matrix as well as sensitivities, log-scaled sensitivities (elasticities) and arcsine-scaled ($\sin^{-1}\sqrt{\theta}$) sensitivities. This latter scaling has been shown to be a reasonable scaling for parameters bounded by 0 and 1 (Link and Doherty 2002), as are all the parameters in our model.

To test whether parameter sensitivities and their associated process variances were negatively correlated, we correlated arcsine-scaled sensitivities and arcsine-scaled temporal process variance estimates, using a Pearson's correlation coefficient.

To test whether reproductive success, juvenile survival, adult survival rates, as well as age-specific breeding probabilities were lower during El Niño years than



$$\begin{vmatrix} F_0 & F_1 & F_2 & F_3 & F_4 & F_5 & F_A \\ G_0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_4 & 0 & 0 \\ M_0 & M_1 & M_2 & M_3 & M_4 & M_5 & P_A \end{vmatrix}$$

Fig. 1. The life-cycle graph and stage-classified, post-breeding, population projection matrix for red-tailed tropicbirds. Stage 0-yearlings; stage 1 – 1-year-olds; stage 2 – 2-year-olds; stage 3 – 3-year-olds; stage 4 – 4-year-olds; stage 5 – 5-year-olds; stage A – adults. P_A indicates adult survival. G_x indicates transition from stage x to x+1 as a function of probabilities of survival and not breeding. M_v indicates maturation from prebreeder age v including probabilities of survival and age-specific breeding. F_v indicates fecundity of tropicbirds of age v including probability of survival, age-specific breeding and reproductive success. See Table 1 for further details.

during non-El Niño years, we performed z-tests as available in Program Contrast (Hines and Sauer 1989).

Results

Model selection and parameter estimates

The model that best fitted our data was a model with a time-invariant transient response ($\gamma = 0.905$), but with time dependence in adult and pre-breeder survival estimates ($\varphi_i^{(k+)}$ and $\varphi_i^{(0)}$), probability of recapture (p_i^{k+}), direct capture probability (p_i') and the age-specific breeding probabilities ($\alpha_i^{(v)}$) for ages 1 to 5. Our estimate of overdispersion (based on a χ^2 goodness-of-fit test) was 1.78. All other models had $\Delta QAIC_c$ rankings > 11. Annual estimates of reproductive success, survival, capture probabilities, and age-specific breeding probabilities are given in Table 2–5, respectively.

After examining parameter estimates from this model, we noticed that many estimates of $\alpha_i^{(5)}$ were near boundaries of 0 or 1 (Table 5). We further attempted to model this parameter as being equal to $\alpha_i^{(4)}$. However, this model did not fit as well ($\Delta QAIC_c = 11.3$). As noted in methods, we also computed estimates from reduced-parameter (time-constant) models for use with projection matrix computations. We note that time-constant parameters fit well in the context of a population matrix model in which rates are considered to be constant and which are projected into the future.

Tropicbirds produce fledglings from 78.0% ($S\hat{E} = 2.7\%$) of the nests, a rate that varied little (Table 2). Adults had, on average, a 6% higher annual survival probability than pre-breeders (0.85 and 0.80 respectively; Table 3). Annual, adult, indirect probabilities of recaptures ranged from 0.27 to 0.65 (Table 4). Age-specific first-time breeding probabilities increased with age from a very low probability (0.004) of breeding at age 1 to 0.457 at age 4. The average estimated probability of breeding at age 5, if a bird had not bred yet, was 0.438. Although the $\alpha_i^{(5)}$ estimates are unbiased, the associated variance estimates are not because many of the estimates are near the boundaries. Problems in estimating this parameter are most likely due to the fact that by age 5 (or 6) there are few birds from a cohort that have both

Table 1. Parameters used in the post-breeding-survey, female-only population matrix model.

Parameter	Definition	Function
F_0	Fecundity at age 1	$\varphi^{(0)}\ \alpha^{(1)}\ C\ R$
F_1	Fecundity at age 2	$\varphi^{(0)}\ \alpha^{(2)}\ C\ R$
F_2	Fecundity at age 3	$\varphi^{(0)}\ \alpha^{(3)}\ C\ R$
F_3	Fecundity at age 4	$\varphi^{(0)}\ \alpha^{(4)}\ C\ R$
F_4	Fecundity at age 5	$\varphi^{(0)}\ \alpha^{(5)}\ C\ R$
F_5	Fecundity at age 6	$\varphi^{(0)}\ C\ R$
F_A	Adult fecundity	$\varphi^{(k+)}\ C\ R$
G_0	Probability of surviving and growing from a nestling to a non-breeder of age 1.	$\varphi^{(0)}\ (1-\alpha^{(1)})$
G_1	Probability of surviving and growing from a non-breeder of age 1 to a non-breeder of age 2.	$\varphi^{(0)}\ (1-\alpha^{(2)})$
G_2	Probability of surviving and growing from a non-breeder of age 2 to a non-breeder of age 3.	$\varphi^{(0)}\ (1-\alpha^{(3)})$
G_3	Probability of surviving and growing from a non-breeder of age 3 to a non-breeder of age 4.	$\varphi^{(0)}\ (1-\alpha^{(4)})$
G_4	Probability of surviving and growing from a non-breeder of age 4 to a non-breeder of age 5.	$\varphi^{(0)}\ (1-\alpha^{(5)})$
P_A	Probability of adult survival.	$\varphi^{(k+)}$
M_0	Probability of surviving and maturing at age 1.	$\varphi^{(0)}\ \alpha^{(1)}$
M_1	Probability of surviving and maturing at age 2.	$\varphi^{(0)}\ \alpha^{(2)}$
M_2	Probability of surviving and maturing at age 3.	$\varphi^{(0)}\ \alpha^{(3)}$
M_3	Probability of surviving and maturing at age 4.	$\varphi^{(0)}\ \alpha^{(4)}$
M_4	Probability of surviving and maturing at age 5.	$\varphi^{(0)}\ \alpha^{(5)}$
M_5	Probability of surviving and maturing at age 6.	$\varphi^{(0)}$

Notes: estimates of average annual prebreeding survival ($\hat{\varphi}^{(0)} = 0.804$), average annual adult survival ($\hat{\varphi}^{k+1} = 0.849$), clutch size ($\hat{C} = 0.5$; corrected for females only), average reproductive success ($\hat{R} = 0.780$), and age-specific breeding probabilities for 1-, 2-, 3-, 4- and 5-year-old birds ($\hat{\alpha}_.^{(0)} = 0.004$, $\hat{\alpha}_.^{(2)} = 0.025$, $\hat{\alpha}_.^{(3)} = 0.252$, $\hat{\alpha}_.^{(4)} = 0.457$, $\hat{\alpha}_.^{(5)} = 0.438$) are used in the model.

Table 2. Annual reproductive success of red-tailed tropicbirds.

Year	Number of nests receiving an egg	Proportion fledging	SÊ
1992	740	0.770	0.015
1993	385	0.779	0.021
1994	520	0.790	0.018
1995	650	0.731	0.017
1996	430	0.821	0.018
1997	520	0.800	0.018
1998	230	0.791	0.027
1999	220	0.759	0.029
mean		0.780	

Notes: reproductive success was measured as the proportion of nests receiving an egg which producing a fledgling (tropicbirds lay only one egg; data from USFWS).

Table 3. Annual survival estimates of prebreeding ($\hat{\varphi}_i^{(0)}$) and adult ($\hat{\varphi}_i^{(k+)}$) red-tailed tropicbirds. Means are weighted means derived from a time-invariant model.

Year	$\hat{\varphi}_i^{(0)}$	SÊ	$\hat{\varphi}_i^{(k+1)}$	SÊ
1983	0.65	0.16	0.94	0.05
1984	0.89	0.21	0.97	0.02
1985	0.79	0.18	0.96	0.01
1986	0.81	0.18	0.93	0.01
1987	0.78	0.17	0.92	0.01
1988	0.81	0.18	0.92	0.01
1989	0.90	0.20	0.94	0.01
1990	0.76	0.17	0.86	0.01
1991	0.95	0.22	0.87	0.02
1992	0.77	0.18	0.88	0.02
1993	0.79	0.18	0.85	0.02
1994	0.82	0.19	0.91	0.02
1995	0.70	0.17	0.89	0.02
1996	1.00	0.37	0.92	0.03
1997	0.25	0.01	0.80	0.03
mean	0.80		0.85	

Table 4. Annual direct capture probabilities ($\hat{p}_i'$) and indirect capture probabilities ($\hat{p}_i$) of tropicbirds. Means are weighted means derived from a time-invariant model.

Year	$\hat{p}_i'$	SÊ	$\hat{p}_i$	SÊ
1984	0.48	0.06	1.00	0.00
1985	0.48	0.02	0.46	0.08
1986	0.52	0.02	0.39	0.02
1987	0.66	0.02	0.65	0.02
1988	0.37	0.01	0.41	0.02
1989	0.50	0.02	0.37	0.01
1990	0.50	0.02	0.45	0.01
1991	0.55	0.01	0.41	0.01
1992	0.37	0.01	0.32	0.01
1993	0.57	0.02	0.51	0.01
1994	0.38	0.01	0.36	0.01
1995	0.41	0.01	0.30	0.01
1996	0.44	0.02	0.27	0.01
1997	0.52	0.02	0.33	0.01
1998	0.37	0.02	0.33	0.01
mean	0.48		0.44	

Notes: the direct capture probability is the probability of recapture at time i for birds caught at time $i-1$ and corresponds to a trap response. The indirect capture probability is the probability of recapture at time i for birds not captured at time $i-1$.

survived and not yet returned to breed. To better estimate the biological variance in which we were most interested, we decomposed the total variance among the annual estimates of reproductive success, survival, and age-specific breeding probabilities into biological process variation and sampling variation using methods described in Link and Nichols (1994) and Gould and Nichols (1998; Table 6). Overall, our parameter estimates were fairly stable, with the exception of $\alpha_i^{(5)}$ (probability of breeding for the first time at age 5). Since we had no confidence in the estimated temporal variance for $\alpha_i^{(5)}$, we did not decompose this estimate and excluded it from correlative analyses (below).

Matrix model

Using average estimates from the above analysis, and the matrix model as outlined in Fig. 1 and Table 1, we estimate the dominant eigenvalue (λ or population growth rate) to be 1.004 and calculated the sensitivity of λ to underlying vital rates using unscaled sensitivity values as well as log-scaled (elasticity) and $\sin^{-1}$-scaled sensitivities (Table 7). All three scales produced similar qualitative rankings of sensitivities. λ was most sensitive to survival, in particular adult survival. λ was less sensitive to reproductive success and least sensitive to age-specific breeding probabilities. We feel the $\sin^{-1}$-scaled sensitivities are the most appropriate for inter-parameter comparison and rankings due to the fact that all of our parameter values are bounded by 0 and 1 (Link and Doherty 2002). Using this particular scale, λ was about as sensitive to pre-breeding survival (0.202) as to adult survival (0.234), a result that differed somewhat from that obtained using a log-scale (0.420 vs 0.577).

Evidence was somewhat consistent with our prediction that the variables to which λ was most sensitive (i.e. survival) were also the variables with the least process variance. The Pearson correlation between $\sin^{-1}$-scaled sensitivities and estimated $\sin^{-1}$-scaled process variances was negative as predicted (-0.31), a result not seen in the correlation between log-scaled sensitivity and total variance (0.03), the correlation used in previous studies (Pfister 1998). However neither of these correlations (using the $\sin^{-1}$-scaled) was significantly different from zero at the 0.05 alpha level ($P = 0.49$ and 0.95 respectively). It should be noted that pre-breeding survival, reproductive success, as well as age-specific breeding probabilities for age 1 and 2 had smaller estimated process variances than adult survival (Table 6). The other three parameters had process variance estimates below zero (Table 6).

Results did not support our predictions that the variables to which λ was least sensitive, (and which we thought would have the highest process variance), would be the variables most affected by El Niño events. Using a

Table 5. Estimated age specific breeding probabilities ($\hat{\alpha}_i^{(v)}$) for tropicbirds aged 1–5. Means are weighted means derived from a time-invariant model.

Year	Age (years)									
	1		2		3		4		5	
	$\hat{\alpha}_i^{(1)}$	$S\hat{E}$	$\hat{\alpha}_i^{(2)}$	$S\hat{E}$	$\hat{\alpha}_i^{(3)}$	$S\hat{E}$	$\hat{\alpha}_i^{(4)}$	$S\hat{E}$	$\hat{\alpha}_i^{(5)}$	$S\hat{E}$
1984	0.003	0.002								
1985	0.002	0.001	0.065	0.008						
1986	0.001	0.001	0.065	0.008	0.404	0.115				
1987	0.010	0.003	0.037	0.009	0.282	0.033	0.425	0.161		
1988	0.005	0.001	0.045	0.010	0.571	0.073	0.827	0.098	0.423	0.297
1989	0.002	0.001	0.035	0.007	0.636	0.075	0.463	0.174	0.000	0.660
1990	0.010	0.003	0.065	0.008	0.335	0.039	0.399	0.190	0.260	0.290
1991	0.001	0.001	0.045	0.010	0.258	0.033	0.598	0.079	0.593	0.272
1992	0.002	0.001	0.037	0.009	0.438	0.046	0.827	0.091	1.000	0.243
1993	0.005	0.001	0.065	0.008	0.307	0.031	0.236	0.077	0.000	0.558
1994	0.005	0.001	0.035	0.007	0.518	0.054	0.827	0.092	1.000	0.132
1995	0.005	0.001	0.035	0.007	0.345	0.042	0.642	0.132	0.000	0.636
1996	0.006	0.004	0.035	0.007	0.475	0.058	0.731	0.104	1.000	0.406
1997	0.010	0.003	0.005	0.006	0.311	0.132	0.676	0.127	0.979	0.354
1998	0.005	0.001	0.045	0.010	0.250	0.157	0.621	0.364	0.429	0.363
mean	0.004		0.025		0.252		0.457		0.438	

Notes: all birds are assumed to breed at age 6.

Table 6. Parameter estimates ($\hat{\theta}$), total estimated temporal variance (S^2), average sampling variance ($\bar{\hat{\sigma}}^2_{xx}$), sampling covariance ($\bar{\hat{\sigma}}^2_{xy}$), biological process variance ($\hat{\tau}^2$) and $\sin^{-1}\sqrt{\sigma}$-scaled $\tau^2(\tau^2/\theta(1-\theta))$ for pre-breeder survival ($\hat{\varphi}^{(0)}$), adult survival ($\hat{\varphi}^{(k)}$), age-specific breeding probabilities ($\hat{\alpha}^{1-5}$) and reproductive success (R).

Parameter	$\hat{\theta}$	S^2	$\bar{\hat{\sigma}}^2_{xx}$	$\bar{\hat{\sigma}}^2_{xx}$	$\hat{\tau}^2$	$\hat{\tau}^2/\theta(1-\theta)$
$\hat{\varphi}^{(0)}$	0.804	0.02943	0.04958	−0.00184	0†	0
$\hat{\varphi}^{(k+)}$	0.849	0.00208	0.00044	−0.00001	0.00163	0.01878
$\hat{\varphi}^{(1)}$	0.004	0.00001	0.00001	−0.00035	0†	0
$\hat{\varphi}^{(2)}$	0.025	0.00028	0.00006	0.00001	0.00023	0.00547
$\hat{\varphi}^{(3)}$	0.252	0.01552	0.00959	0.02515	0.03108	0.13006
$\hat{\varphi}^{(4)}$	0.457	0.03654	0.02261	0.00036	0.01429	0.05985
$\hat{\varphi}^{(5)}$	0.438	‡	‡	‡	‡	‡
$\hat{R}$	0.780	0.00075	0.00044	§	0.00031	0.00181

†We report estimates of zero where negative variance component point estimates were obtained. Mathematically negative variances can be calculated, but they have no biological significance.

z-test as available in Program Contrast (Hines and Sauer 1989), we found adult survival was slightly lower when averaged across El Niño years (0.87) than in non-El Niño years (0.92, $\chi^2 = 23.37$, df = 1, $P < 0.01$, Fig. 2). The same trend was also seen in juvenile survivorship with point estimates of survival during El Niño years on average 0.10 lower than during non-El Niño years (0.71 vs 0.81, Fig. 2). This difference, however, was not significant ($\chi^2 = 0.91$, df = 1, $P = 0.34$). Differences were also detected in direct (0.49 vs 0.45, $\chi^2 = 9.99$,

Table 7. Sensitivities of λ to demographic parameters used in the population matrix model.

Parameter	Sensitivity		
	Unscaled	Log-scale	$\sin^{-1}$-scale
Pre-breeding survival ($\hat{\varphi}^{(0)}$)	0.529	0.420	0.202
Adult survival ($\hat{\varphi}^{(k+1)}$)	0.682	0.577	0.234
1-year-old breeding probability ($\hat{\alpha}^{(1)}$)	0.108	0.000	0.007
2-year-old breeding probability ($\hat{\alpha}^{(2)}$)	0.067	0.002	0.010
3-year-old breeding probability ($\hat{\alpha}^{(1)}$)	0.043	0.011	0.018
4-year-old breeding probability ($\hat{\alpha}^{(4)}$)	0.023	0.011	0.011
5-year-old breeding probability ($\hat{\alpha}^{(5)}$)	0.007	0.003	0.003
Reproductive success ($\hat{R}$)	0.136	0.105	0.054

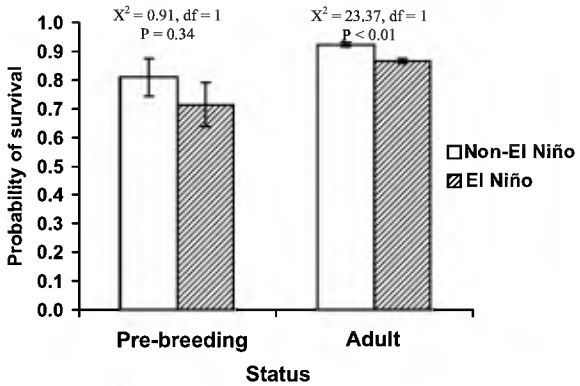


Fig. 2. Adult survival rates are higher during non-El Niño years than during El Niño years. This same trend is detected for pre-breeders but not significantly so. Means ± SE (sampling variance), and results of z-tests (Hines and Sauer 1989) are shown.

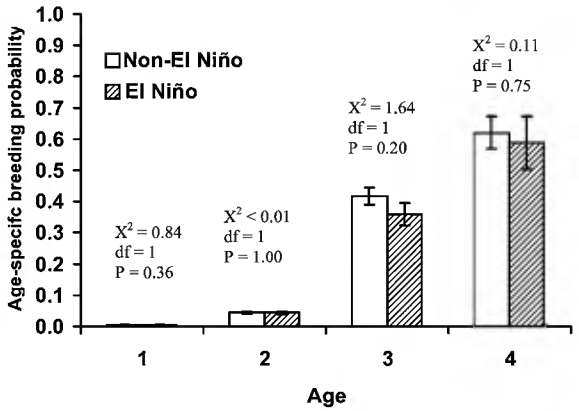


Fig. 4. No differences between age-specific breeding probabilities of red-tailed tropicbirds during El Niño event-years and non-El Niño event years were detected. Means ± SE (sampling variance), and results of z-tests (Hines and Sauer 1989) are shown.

df = 1, $P < 0.01$) and indirect (0.41 vs 0.47; $\chi^2 = 16.77$, df = 1, $P < 0.01$) recapture probabilities (Table 4). No differences between El Niño years and non-El Niño years were seen in reproductive success (0.78 in both, Fig. 3) or in age-specific breeding probabilities (Fig. 4).

Discussion

Although much discussion has taken place concerning the relationships of vital rates, and temporal variation in these rates, to population growth rate (Gaillard et al. 1998, Pfister 1998, Heppell et al. 2000), proper estimation of these parameters has been rare (Gaillard et al. 1998, Wisdom et al. 2000). We employed recent methodological advances in estimating parameters, their temporal variances, and their scaled sensitivities to test predictions about population growth rate of red-tailed tropicbirds. We will discuss our demographic parameter estimates, the population matrix model, predictions concerning rates to which λ is most sensitive, the correlations of these sensitivities with temporal variances, and finally predictions concerning El Niño events.

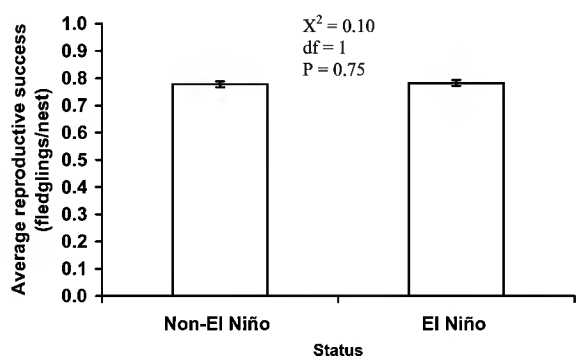


Fig. 3. There was no detectable difference in average reproductive success of red-tailed tropicbirds during non-El Niño years and El Niño years. Means ± SE (sampling variance), and results of z-tests (Hines and Sauer 1989) are shown.

Parameter estimates

We modeled survival and age-specific breeding probabilities using newly developed mark–recapture methods (Spendelow et al. 2002, Williams et al. 2002). Because many seabirds are not seen from fledging until they first breed, and because not all birds in a cohort first breed at the same age, the estimation of pre-breeding survival has been difficult in the past. Our estimates of age-specific breeding probabilities take into account the probability of survival and recapture, an advance over previous ad hoc approaches, such as examining the age distribution of birds first observed breeding, which are confounded with survival and detection (Williams et al. 2002). Results from these analyses indicate that adult survival is high (> 85%, Table 3), an inference common to other studies of long-lived seabirds (Brichetti et al. 2000, Appendix 2 in Schreiber and Burger 2001). Pre-breeding survival (annual survival during the period from fledging to breeding) was 0.05 lower than adults, with tropicbirds having an increasing probability of first breeding from age 1 to age 4 (Table 5). The probability of first breeding at ages one or two was very low (< 0.03), with the probability of first breeding increasing at ages 3 and 4 (0.25–0.46). Our results, as well as those of Spendelow et al. (2002), demonstrate an increase in first-time breeding probabilities with age. This modeling framework for age-specific breeding probabilities should allow more rigorous testing of hypotheses concerning age and reproduction in birds (Forslund and Pärt 1995).

Average annual reproductive success of tropicbirds over the 17-year study was 78% (73–82%, Table 2) which is relatively high and invariant compared to that found in related tropical seabird species: 10–70% in masked boobies (*Sula dactylatra*), 10–75% in brown boobies (*S. leucogaster*), 23% in blue-footed boobies (*S. nebouxii*), 10–80% in red-footed boobies (*S. sula*, Nelson 1979).

Sensitivities and variances

We constructed a population matrix model using averaged estimates from our above modeling to test the prediction that asymptotic λ is most sensitive to parameters affecting survival and less so to those affecting reproductive success. In performing this sensitivity analysis we scaled sensitivity by variance for parameters that are bounded by 0 and 1. If this is not done, and elasticities are used for ranking, then different conclusions may be drawn depending on whether mortality or survival is used to parameterize the population model (Olesiuk et al. 1990, Brault and Caswell 1993, Hunter et al. 2000). The scaling that we believe to be most reasonable is a $\sin^{-1}$-scaled, rather than an unscaled or log-scaled, sensitivity (Link and Doherty 2002). When using this scale (Table 7), λ is most sensitive to adult survival, followed closely by pre-breeding survival. λ was much less sensitive to reproductive success and age-specific probabilities of breeding. Results thus supported the prediction based on previous work with log-scaled sensitivities (Pfister 1998, Heppell et al. 2000).

Results also supported the prediction that the scaled sensitivities would be negatively correlated with process variances, although not unequivocally. This is one of the few instances (Franklin et al. 2000), that estimated process variances have been used in such a comparison, even though the fact that sampling variances could distort past analysis has been recognized (Gaillard et al. 1998, Wisdom et al. 2000). Although the Pearson correlation coefficient was negative, the parameter (adult survival) to which λ was most sensitive had a higher process variance than some parameters to which λ was less sensitive (reproductive success, breeding probabilities at age 1 and 2, pre-breeder survival). If one strongly believes in the negative correlation, then one interpretation of this result is that sensitivities may be good indicators of past action of stabilizing selection pressure and that the reduced variation may be an indication of canalization (Stearns and Kawecki 1994, Pfister 1998), as has been suggested in past life history studies.

However, in these past analyses in which means and variances were not transformed to be independent of each other, there is an alternative interpretation that there is no selection for reduced variation. If a rate, such as survival in long-lived animals, is selected to be high, then by definition the variance will be low. Mathematically, there is little possibility of variation given that average survival is near the upper bound of one. In contrast, measures of reproductive success can vary over a wider range. Thus, this past negative relation between sensitivities and variances of parameters in long-lived animals may be an artifact of selection for high mean survival rates alone, and not selection for low variances independent of the mean (canalization). If this is indeed the case, then one tenet of life-history theory should be re-addressed with proper estimation and scaling as we have done here.

Given the fact that previous studies have not used robust estimation and scaling, and if one does not think the correlation we found is strong, and if one focuses on the relatively large process variation in adult survival and the result that effects of El Niño were most strongly seen in adult survival (below) then there is little support for this second prediction.

Effects of El Niño events

We examined vital rates for evidence of variation in conjunction with the occurrence of El Niño events, predicting negative effects in tropicbirds would be detected first in the least sensitive vital rates (and thought to be most variable); those associated with reproductive success. However, results did not support this prediction in this population. We detected no significant difference in reproductive success (Fig. 3), nor in age-specific breeding probabilities (Fig. 4), between El Niño years and non-El Niño years. However we did detect significant differences in survival with adult survival being lower during El Niño years (0.87 vs 0.92, $P < 0.01$). The same trend was also seen in pre-breeders, but the difference was not significant (0.71 vs 0.81, $P = 0.31$, Fig. 2).

Massive reproductive failure has been the most often reported result of El Niño events (Schreiber and Schreiber 1984, 1989, Hodder and Graybill 1985, Hatch 1987, Anderson 1989, Boersma 1998), and this did not occur during this study. Even though Johnston Atoll is located in the central Pacific, the atoll may be outside the area of the most severe effects of El Niño. Many of the seabirds on Johnston Atoll seem to experience mild to no effects on reproduction with the exception of sooty terns (*Sterna fuscata*) which have undergone massive reproductive failures on Johnston Atoll during El Niño events. Sooty terns may be more susceptible to food shortages than tropicbirds.

The absence of a strong effect in reproductive success on Johnston Atoll tropicbirds was unexpected. It may be that the birds on Johnston Atoll are foraging at upwellings caused by the north equatorial current hitting the Atoll and surrounding seamounts, versus feeding at upwellings caused by current interfaces. With a wind-

driven change in circulation, upwellings caused by current interfaces may disappear, but sea mounts may still cause upwellings. We do know that red-footed boobies feed at a set of sea mounts just south of the atoll (satellite telemetry: Schreiber 2000), but we do not yet know if tropicbirds feed in the same area.

Fewer studies have been able to examine survival, which requires populations of marked birds and more sophisticated modeling efforts (Brichetti et al. 2000, Beadell et al. 2003). Massive declines in adult populations have been viewed as a result of decreased survival, although permanent emigration always remains a possibility. The 1982–83 El Niño event caused such a decline in the adult population of Galapagos penguins (*Spheniscus mendiculus*) in the Galapagos (Merlen 1985); in masked boobies (*Sula dactylatra*) and sooty terns (*Sterna fuscata*) on Christmas Island (Schreiber and Schreiber 1984); in cormorants, murres and guillemots in California (Ainley et al. 1988); and has led to the generalization that all El Niño events would have such effects on reproductive success and survival.

Our finding of decreased survival during El Niño events without a decrease in reproductive-related parameters is counter to life-history theory and may suggest that perhaps we do not know enough about the tropicbirds' endocrine-controlled physiological systems. It may be behaviorally impossible for tropicbirds to desert chicks during poor years (Schreiber 1994) and thus pay the cost in terms of survival.

In conclusion, we make three improvements to previous work. First we improve upon ad hoc estimates of survival and age-specific breeding probabilities, utilizing mark-recapture models that account for capture probabilities < 1. Second we focus on estimates of biological process variation, and factor out sampling variation in our analyses. Lastly we utilize variance-based scaling in our sensitivity comparisons and correlations with temporal variances. Using these improvements we support our first prediction that λ is most sensitive to survival rates. We find equivocal support for the prediction that the rates to which λ is most sensitive will have the smallest temporal variances. However these predictions are derived from past work without proper scaling in sensitivities and proper partitioning of variances and we suggest that previous support for the second prediction necessarily results from a high survival estimate near the upper boundary of 1 and should not be interpreted necessarily as a result of canalization. This tenet of life history theory should be revisited. Results did not support our third prediction that effects of environmental stochasticity (El Niño events) would be most likely to be detected in vital rates to which λ was least sensitive.

El Niño events have the potential to affect the demography of seabirds in four basic ways. Severe local effects can extirpate a colony. Unusual wind patterns and storms can cause range expansion through extralimital dispersion. El Niño events can cause anything up to complete reproductive failure for the year. And lastly, these events can cause significant adult mortality. The finding in this study that there was little evidence for effects on reproduction, but some evidence for effects on survival, is unexpected. Similar analyses to ours using comparative data-sets on other seabirds; within and among orders, and in other locations, are needed to understand environmental effects and to assess the generality of our findings

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