

## Resolving the population status of Ascension Frigatebird *Fregata aquila* using a 'virtual ecologist' model

NORMAN RATCLIFFE,<sup>1\*</sup> TARA PELEMBE<sup>2</sup> & RICHARD WHITE<sup>2</sup>

<sup>1</sup>RSPB Scotland, 10 Albyn Terrace, Aberdeen, AB10 1YP, UK

<sup>2</sup>Ascension Island Conservation Office, Georgetown, Ascension Island, South Atlantic

The Ascension Frigatebird is an island endemic whose conservation status was subject to confusion owing to difficulties in counting and misinterpretation of data. Accurate nest counts for this species are problematic owing to their extremely prolonged breeding seasons, high nest failure rates, turnover of individuals at nest-sites, replacement laying and biennial breeding. We conducted repeated complete censuses of Ascension Frigatebird eggs at the species' sole colony of Boatswainbird Island, and collected data on laying phenology and nest survival rates within sample quadrats, throughout the 2001 and 2002 breeding seasons. We used these data to develop an individual-based model that predicted the number of Frigatebird nests present on each day an actual census occurred assuming an arbitrary 1000 breeding females bred there. We then divided the number of nests counted in these virtual censuses by 1000 to quantify bias, and used this figure to correct real census totals. The model revealed that the population numbered *c.* 6250 breeding females and *c.* 9350 mature females in 2001–2, and that numbers have not changed significantly since the late 1950s. Productivity, at 0.34 chicks/pair, was high compared to previous studies of Ascension Frigatebirds and most of those of congeners elsewhere.

**Keywords:** census methods, frigatebird, tropical seabirds, virtual ecologist model.

The Ascension Frigatebird *Fregata aquila* is endemic to Ascension Island in the tropical South Atlantic (7°57'S, 14°22'W) and breeds at a single colony on the summit plateau of Boatswainbird Island (BBI). While their breeding range is well known, their status and trends are subject to considerable confusion. Stonehouse and Stonehouse (1963) judged that around 10 000 breeding birds occupied the sole colony on Boatswainbird Island (BBI) in the 1950s based on impressions gained during a 2-year study of their breeding biology, whereas Blair (1989) cited snapshot counts of 1000–2500 breeding birds in the late 1980s. This led Collar *et al.* (1994) to list the species as 'Critically Endangered' based on population decline but, as this could have been due to differences in detection rate among surveys, Birdlife International (2000) demoted its threat status to 'Vulnerable' based on limited geographic range.

Counts of nests at the peak of incubation activity are the most common means of censusing seabirds (Mitchell *et al.* 2004), but will seriously underestimate the status of some tropical species because nesting seasons are protracted (Dorward 1963, Snow 1965, Diamond 1975a, Brooke 1995), such that many nests will fledge prior to, or be initiated after, the peak census. Furthermore, nest failure rates are often high (Stonehouse 1963, Nelson 1975, Phillips 1987, Reville 1991), and so breeding attempts may be omitted from counts owing to them failing prior to a census and the nest-site subsequently becoming either undetectable or occupied by another pair (Reville 1983). Repeated counts of eggs throughout the season, separated by the incubation period to avoid double counting of individual nesting attempts, can be used to overcome these problems partially (Ashmole *et al.* 1994). Even so, pairs may still lay and fail between counts such that they are omitted from census totals, or relay in the same year following failure (Stonehouse 1963) such that they may be counted twice. Finally,

\*Corresponding author.

Email: norman.ratcliffe@rspb.org.uk

successful female frigatebirds *Fregata* ssp. breed biennially (Diamond 1972, 1975b, Trivelpiece & Ferraris 1987, Osorno 1999), which means that females breeding successfully in the previous season are not detected by nest counts. Accurately censusing Ascension Frigatebirds involves overcoming all of the biases described above, and so the previous confusion over their status and trends is understandable.

Notwithstanding these problems, accurate counts of breeding Ascension Frigatebirds are urgently required to assess their conservation status with confidence. Furthermore, a baseline count is required to quantify population trends following a restoration project that removed feral cats *Felis catus* from the main island between 2002 and 2004 (M. Bell unpubl. data). Ascension Frigatebirds were once found throughout the coastal plain of Ascension, but predation by feral cats introduced in 1815 restricted them to the cat-free island of BBI where competition for nesting space regulates numbers (Ashmole *et al.* 1994). Conservationists predict that Ascension Frigatebirds will colonize the mainland in response to removal of cats, and that the population will grow owing to relaxation of density-dependent nest-site competition (Ashmole *et al.* 1994), but a robust means of estimating population size and trends is needed to test this empirically.

In this paper, we use a 'virtual ecologist' model parameterized with estimates of nesting phenology, rates of daily nest survival, renesting and biennial breeding to estimate the likelihood of counting a female Frigatebird's nesting attempt using the adopted census methods. We use this value to correct the number of Ascension Frigatebird eggs counted on BBI during 1958, 2001 and 2002 and estimate population status and changes in numbers over the intervening period.

## METHODS

### Study site and field methods

BBI is an islet to the east of Ascension Island that rises steeply to a summit plateau (3 ha, 104 m asl) on which the frigatebird colony is situated. We censused all eggs present on the summit plateau of BBI by walking through the colony, four in line abreast, and tilting apparently incubating birds upward using the tip of their tail streamer to confirm whether they were sitting on an egg (birds did not leave their nest following this treatment). We assumed all birds incubating during the census were detected, which is

realistic as they are large, black birds nesting on open, white ground. We repeated censuses every 50–60 days from May 2001 to December 2002, thus spanning the majority of two successive nesting seasons. The incubation period for Ascension Frigatebird is 44 days (Stonehouse & Stonehouse 1963), and so any eggs censused previously would have hatched or failed by the following census, which avoids double counting of nesting attempts.

We placed 10 quadrats 5 × 5 m throughout the colony in areas of varying nesting density and visited them every 10–20 days. On each visit, we marked new nests with a numbered peg, marked the egg with indelible ink, and recorded the fate of nests that were marked previously. Chicks were aged on first encounter according to their appearance following the descriptions in Stonehouse and Stonehouse (1963). Chicks older than 50 days can shuffle several metres from their nest-site, and so we injected any chicks approaching this age in the nape of the neck with a passive induced transmitter (PIT) tag, and used a hand-held tag reader to confirm their identity on subsequent visits.

### Statistical modelling

We calculated annual raw census totals by summing all complete egg counts within each year. We described laying phenology by calculating the number of new nests initiated in the quadrats between each visit and dividing it by the duration of the interval to estimate the daily rate of laying. We summed these within calendar months and divided each monthly total by the total number of eggs laid to produce a histogram of the percentage of eggs laid in each month.

We estimated daily nest survival following the Stephens method described in Rotella *et al.* (2004), which uses a logistic regression approach to model survival on each day the nest is monitored in relation to explanatory covariates. We separated survival estimation for eggs and chicks to avoid the requirement for complex interaction terms between stage and covariates. The explanatory covariates we modelled at the egg stage were linear, quadratic and cubic (on a logit scale) effects of date and year; during the chick stage the age of the chick was also included. Laying seasons were assumed to start on 1 March (see Results), and so coding of year and date variables started on 1 March and ended on 28 February in the following calendar year. Reference to year hereafter refers to the year in which the nesting season started. We selected the model with the lowest AIC value, unless the delta AIC value differed from a model

with fewer parameters by less than two units (Burnham & Anderson 2002).

### Simulation modelling

We adopted a 'virtual ecologist' approach (Grimm *et al.* 1999) to quantify bias in the raw census totals and hence calculate accurate population estimates with confidence intervals. This was designed to correct for all of the biases described in the introduction, and also for double-counting of individual nesting attempts in the 1958 census as this was conducted at intervals less than the average incubation period (Stonehouse & Stonehouse 1963).

We focused on estimating numbers in terms of breeding and mature females because their gender limits the number of eggs laid; males are more likely to breed annually (Diamond 1972, Osorno 1999) and so have an excess non-breeding component. Similarly, the approach outlined is unable to provide estimates of numbers of pre-breeders. Data from counts of nests and studies of breeding biology would have to be supplemented by those from capture-mark-recapture studies before estimates of the number of mature males and pre-breeders of either gender would be possible, and this was beyond the scope of this study.

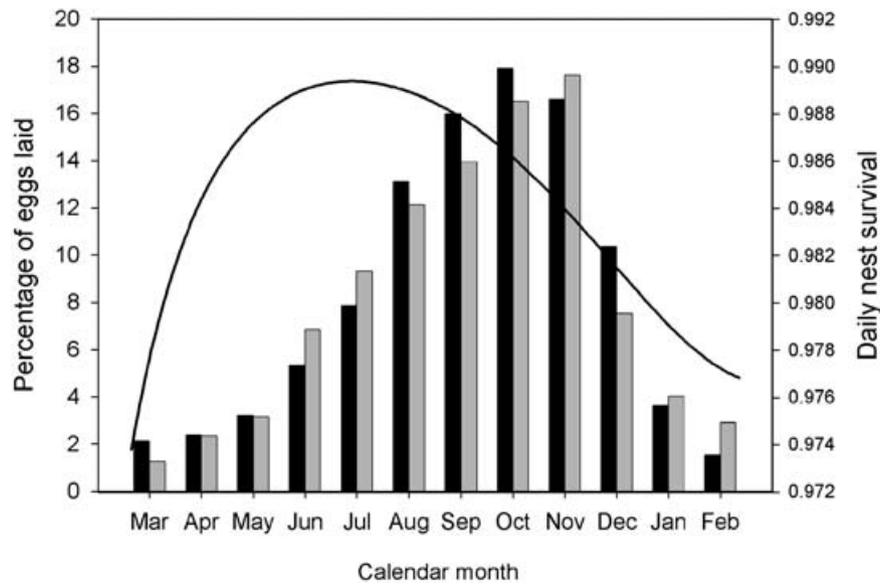
We first developed an individual-based simulation model of a virtual Frigatebird colony comprising 1000 females. This allocated each pair a random start date at which they initiated their first breeding attempt, drawn from a normal distribution defined by the mean first laying date and its standard deviation. The model then assessed whether a nest survived each day of incubation by testing if a random probability was less than the daily egg survival rate until it hatched at 44 days or failed. If the nest hatched, the model subjected the breeding attempt to the daily chick survival rate in a similar manner until it failed or fledged at 180 days. Birds that failed during the egg stage were allowed to relay after a replacement period of three months (Stonehouse & Stonehouse 1963), provided the date relaying was due did not fall after a randomly allocated stop date (the date after which a bird was unable to relay) and they had not laid a replacement clutch previously that year. We estimated the mean start and stop dates and their standard deviations by iteratively varying these values in the model until the predicted monthly laying phenology matched that observed (Ratcliffe *et al.* 2005), and the proportion of failed breeders that relaid equalled 0.25 (the value estim-

ated empirically by Stonehouse and Stonehouse (1963)).

We then assigned a virtual ecologist to conduct counts in the virtual colony on each calendar date that we actually censused BBI to produce a virtual census total for each year. Within the model, this was achieved by adding one to a running total for every Frigatebird nest containing an egg on any census date. We divided this virtual census total by 1000 (the known number of breeding females in the virtual colony) to estimate a detection probability (defined as the likelihood of a female Frigatebird breeding in the current year being included in the census total) for each year. We then divided the real number of Frigatebird eggs counted in a year by this detection probability to calculate the real number of breeding females. This procedure was repeated 10 000 times, with the average of these values being taken as the population estimate in units of breeding females, and the 2.5 and 97.5 percentiles as the lower and upper 95% confidence intervals, respectively.

To estimate status in 1958 we extracted data from Stonehouse and Stonehouse (1963). We took counts of eggs in each month from Figure 1 in that paper and divided these values by 0.60 as the numbers in the survey areas represented 60% of the total. In the absence of details of the actual census dates, we assumed all were taken on the 15th of each month. We adjusted the intercepts of our egg and chick survival rate estimates until the overall success per nesting attempt equalled 0.175, which is intermediate to the 0.15–0.20 chicks per pair estimated during the Stonehouses' study. The significance of change between 1958 and 2001–2 was assessed by inspection of the overlap between the estimates and the bootstrapped confidence intervals.

Female frigatebirds that fledge a chick breed biennially (Nelson 1975, Orta 1992), and so the number breeding in any given year will underestimate the size of the sexually mature population. Calculating the number of mature females requires data on the level of productivity in the previous year and so we could estimate this only for 2002. We used the simulation model to keep a running total of every chick that reached fledging age, and divided this by the number of pairs to calculate a productivity estimate. This was repeated 10 000 times and the mean and standard deviation were taken as productivity with se respectively (note that in bootstrap analyses the sd of resampled values equals the se of the estimate). We then re-ran the previously described nest detection model



**Figure 1.** Monthly frequency distribution of Ascension Frigatebird laying (black bars) compared with the best-fit distribution obtained from the simulation model (grey bars) plotted on the left axis. The seasonal variation in daily nest survival rate at the egg stage (solid line) is plotted on the right axis.

with the addition that females were only allowed to attempt breeding if a randomly selected probability value was greater than the average productivity estimate. The number of mature females was then calculated in the manner described for the number of breeding females. The model assumes that all unsuccessful females breed annually and successful ones biennially. In reality, some birds may breed less frequently than this and so the number of mature females will be underestimated.

All simulation models were run using bespoke programmes written in Microsoft VISUAL BASIC 6.0.

## RESULTS

Ascension Frigatebirds laid eggs all year round, though with a consistent seasonal pattern: a nadir in February rising steadily to a peak in October before declining sharply through December and January (Fig. 1). A start date of 6 September ( $sd = \pm 80$ ) and a stop date of 5 December ( $sd = \pm 5$ ) provided a good fit to the observed pattern of laying (Fig. 1).

The most parsimonious model of egg survival was that of a cubic effect of calendar date, which provided an AIC value over 6 units lower than those including linear or quadratic effects of date (Table 1). Models including year were not supported. The seasonal variation in daily egg survival is shown in Figure 1 and is described by the equation:

**Table 1.** AIC table for Ascension Frigatebird egg survival where Const = constant survival,  $t$  = date (linear),  $t^2$  = calendar date (quadratic),  $t^3$  = calendar date (cubic),  $y$  = year, 'n' is the number of intervals, 'k' is the number of parameters and 'ness' is the effective sample size (Rotella *et al.* 2004). The selected model is in bold text.

Model	n	k	ness	AIC	Delta AIC
<b><math>t^3</math></b>	<b>1265</b>	<b>4</b>	<b>24 867</b>	<b>1512.237</b>	<b>0.000</b>
$t^2$	1265	3	24 867	1518.471	6.233
$t$	1265	2	24 867	1518.710	6.471
$t \cdot y$	1265	3	24 867	1518.978	6.740
$t^2 \cdot y$	1265	5	24 867	1520.878	8.642
$t^3 \cdot y$	1265	5	24 867	1520.878	8.642
Const	1265	1	24 867	1526.487	14.249
$y$	1265	2	24 867	1527.346	15.108

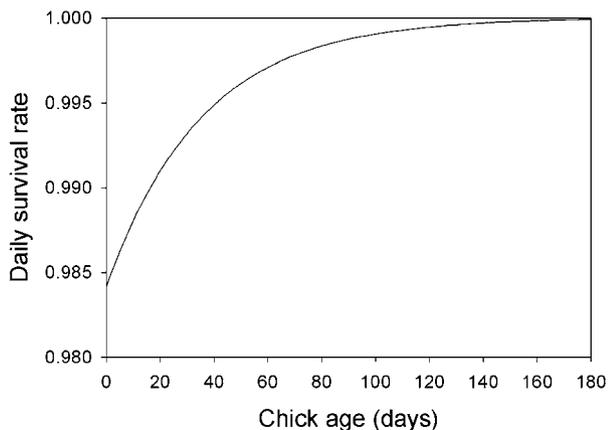
$$S_e = \frac{1}{1 + \exp^{-(3.61+0.016 \cdot t - 8.00E^{-0.05} \cdot t^2 + 1.04E^{-0.07} \cdot t^3)}}$$

where  $S_e$  is egg survival and  $t$  is date in units of days after 28 February. Survival was lowest in January to April when few birds attempted to breed, but increased sharply as laying increased through to July before undergoing a decline prior to the peak of laying (Fig. 1).

The most parsimonious model of chick survival was that including a linear effect of chick age (Table 2). A model that included a linear decline

**Table 2.** AIC table for Ascension Frigatebird chick survival where  $a$  = chick age, Const = constant survival,  $t$  = date (linear),  $t^2$  = date (quadratic),  $t^3$  = date (cubic),  $y$  = season, 'n' is the number of intervals, 'k' is the number of parameters and 'ness' is the effective sample size (Rotella *et al.* 2004). The selected model is in bold text.

Model	n	k	ness	AIC	Delta AICc
$a \cdot t$	1191	3	38 644	584.98	0.00
<b>a</b>	<b>1191</b>	<b>2</b>	<b>38 644</b>	<b>585.44</b>	<b>0.46</b>
$a \cdot t^2$	1191	4	38 644	586.20	1.22
$a \cdot t \cdot y$	1191	4	38 644	586.81	1.83
$a \cdot t^3$	1191	5	38 644	587.36	2.38
$a \cdot y$	1191	3	38 644	587.44	2.46
$t^2$	1191	3	38 644	676.06	91.08
$t^3$	1191	4	38 644	678.02	93.04
$y$	1191	2	38 644	683.89	98.91
$t$	1191	2	38 644	685.75	100.76
Const	1191	1	38 644	688.06	103.08



**Figure 2.** Daily survival rates of Ascension Frigatebird chicks in relation to their age.

with date had an AIC value that was lower by 0.4 units but, as this reduction was less than the 2-unit threshold we adopted, this model was rejected in favour of the age-only model. Models including year or quadratic/cubic effects of date were not supported as they had larger AIC values and more parameters. Based on the parameter estimates from the selected model, daily survival was 0.983 in hatchlings and increased to 100% in birds approaching fledging age (Fig. 2), as described by the equation:

$$S_c = \frac{1}{1 + \exp^{-(4.13 - 0.03 \cdot a)}}$$

**Table 3.** Raw census totals, detection likelihoods and population estimates for Ascension Frigatebirds during 3 years of study.

	Parameter	1958	2001	2002
Breeding females	Raw census total	6388	4222	3701
	Detection probability	1.028	0.689	0.578
	Population estimate	6217	6129	6408
	Lower 95% CI	5981	5848	6047
Mature females	Upper 95% CI	6479	6436	6816
	Detection probability	–	–	0.397
	Population estimate	–	–	9341
	Lower 95% CI	–	–	8587
	Upper 95% CI	–	–	10 113

where  $S_c$  is chick survival and  $a$  is chick age in units of days after hatching.

Productivity for those females attempting to breed, allowing for relaying and appropriately weighted with respect to seasonal variations in egg laying and egg survival, was 0.34 chicks/pair ( $se = \pm 0.07$ ) during 2001 and 2002, and 0.19 ( $se = \pm 0.06$ ) in 1958.

The simulation model outputs are presented in Table 3. The detection likelihoods differed from each other in all years of study, indicating that use of raw census totals would result in biased estimates of both population status and change. In 2001 and 2002, the censuses underestimated the number of breeding females by 31% and 42%, respectively, and the mature population of females in 2002 by 60%. In contrast, the 1958 census overestimated the number of breeding females by 3% due to the interval between surveys being less than the incubation period and consequent double counting of nesting attempts. A single peak count in October 2002 would have underestimated the number of breeding females by 80% and of mature ones by 86%, which emphasizes the folly of attempting to census asynchronously nesting species using uncorrected peak incubation counts.

The number of breeding females on BBI was similar in all years of study and averaged 6250, with inspection of the confidence intervals revealing that there was no significant change in numbers between 1958 and 2001–2 (Table 3). The number of mature females in 2002 was 9341 (Table 3) but could not be calculated for 1958 and 2001 because productivity in the preceding years was unknown.

## DISCUSSION

Our virtual ecologist model has finally allowed the status of Ascension Frigatebird to be resolved at

6250 breeding females and 9341 mature females. Stonehouse and Stonehouse (1963) guessed that around 10 000 birds bred on Ascension and this, whether through good judgement or serendipity, is close to the estimate of 12 500 birds from our model. The results indicate that the snapshot counts of 1000–2500 pairs given by Blair (1989) were underestimates owing to incomplete detection. This confirms that the classification of Ascension Frigatebird as 'Critically Endangered' based on population decline (Collar *et al.* 1994) was unwarranted and that the current classification of 'Vulnerable', based on limited range and a stable population (Birdlife International 2000), is appropriate.

Ashmole *et al.* (1994) hypothesized that competition for predator-free nesting habitat on BBI was limiting the Ascension Frigatebird population. Density-dependent competition for nesting space could reduce overall productivity for two reasons. First, nest usurpation by unpaired males is the main cause of breeding failure in frigatebird species (Stonehouse & Stonehouse 1963, Nelson 1975, Reville 1988, 1991), and competition for sites is likely to explain the decline in nest survival observed during the peak of laying observed in this study (see Results). Secondly, competition for nest-sites during the peak of nesting may force birds to breed at those unfavoured times of year (January–April) when nest survival is poor (see Results). In contrast to other seabird species, Ascension Frigatebirds have yet to recolonize the main island (T. Pelembe unpubl. data) in response to the removal of feral cats but, if they do so, we predict that reduced competition for nesting habitat will result in laying phenology becoming more synchronous and nest survival rates increasing. Both would result in a larger proportion of the population having active nests during the peak of incubation activity, which might have resulted in overestimation of population growth rates had we relied on uncorrected peak nesting counts to monitor the efficacy of the restoration programme.

Changes in the marine environment could result in the population failing to increase as predicted. Ascension Frigatebirds are known to be caught on baited hooks of the local sports fishery which, while insignificant in itself, may indicate vulnerability to bycatch mortality on hooks set by longline fisheries for tuna (Ratcliffe 1999). The 200 nm Exclusive Fishing Zone (EFZ) around Ascension is currently closed, but Ascension Frigatebirds remain potentially vulnerable given that congeners elsewhere are able to forage beyond this range from their colonies

(Weimerskirch *et al.* 2004), and in any case the absence of fisheries protection means that fishing vessels can intrude illegally into the EFZ with impunity. Furthermore, Ashmole *et al.* (1994) expressed concern that tuna fisheries may have depleted the predatory fish that seabirds need to drive their prey to the surface, such that the population might now be regulated by poor food availability rather than lack of breeding space. However, Ascension Frigatebird productivity in 2001–2 was high compared to that in 1958 (Stonehouse & Stonehouse 1963), and many of the studies of congeners elsewhere (see Nelson 1975, Orta 1992, Diamond & Schreiber 2002, Metz & Schreiber 2002 for reviews) which does not support this hypothesis.

Continued monitoring of Ascension Frigatebird population status is clearly essential given the putative benefits of management and the remaining potential threats they may face at sea. The narrow confidence intervals around the baseline population estimates mean that the power to detect trends is reasonably good: numbers will have to change by a mere 6% over any time period to be statistically detectable with an alpha value of 0.05. Given the slow intrinsic rates of population growth typical of seabirds (Croxall & Rothery 1991), such precision is a prerequisite for assessing changes in status during the early stages of the restoration project.

The results show that ignoring bias in raw nest counts is likely to produce inaccurate estimates of status and trends for asynchronously nesting species such as frigatebirds. The virtual ecologist model presented here allows for simultaneous correction of all potential biases inherent in counts of asynchronously nesting seabirds for any census design. We would therefore recommend adoption of this model for censuses of other frigatebird species. Methods may have to be altered slightly before application to frigatebirds nesting in other habitats. For example, birds nesting in tall trees such as on Christmas Island (Nelson 1975) may need to be counted from vantage points, whereas those in mangrove are best counted from kayaks (Burger 2000). Breeding biology data may need to be collected from study plots overlooked by a hide (Reville 1983) for colonies where access is difficult (e.g. mangroves) or where birds are sensitive to disturbance.

The model can also be used to correct biases in censuses of other tropical seabird families that have asynchronous breeding and low nest survival, including White-tailed Tropicbirds *Phaethon lepturus*, that have the further complication of sub-annual breeding

periodicity (Stonehouse 1963, Prys-Jones & Peet 1980). The main drawback of the approach is that obtaining the input parameters such as laying phenology, nest survival and breeding periodicity requires collection of data from a large number of nests during frequent visits throughout the breeding season. Hence, the scope for its application to small colonies, sites that are difficult to access, or studies for which year-round manpower is difficult to muster will be limited.

This project was carried out as part of the Ascension Island Seabird Restoration Project, led by RSPB and funded by the Foreign and Commonwealth Office. We are grateful to Sarah Sanders, Jim Stevenson (RSPB) and Geoff Fairhurst (FCO) for logistic support and advice throughout the project. Mike Bell, David Boyle, Tony Loxton, Fiona Roberts, Allan Bull, Rob Curtis, Georgina Pickerell and Nik Aspey assisted with data collection. We are indebted to Tony Loxton (Dragon Safety Systems) for providing rope access to the summit of BBI, and the crew of 'Wideawake II' for transport between Georgetown and BBI. Stijn Beirrmann (BioSS) and James Pearce Higgins (RSPB) provided advice about implementing the nest survival models in SAS and Alan Burger provided comments on an earlier draft.

## REFERENCES

- Ashmole, N.P., Ashmole, M.J. & Simmonds, K.E.L.** 1994. Seabird conservation on Ascension Island. In Nettleship, D.N., Burger J. & Gochfeld, M. (eds) *Seabirds on Islands: Threats, Case Studies and Action Plans*: 94–121. Cambridge: Birdlife International.
- Birdlife International.** 2000. *Threatened Birds of the World*. Barcelona: Lynx Edicions.
- Blair, M.** 1989. The RAFOS expedition to Ascension Island, 1987. *J. R. Air Force Orn. Soc.* **19**: 1–34.
- Brooke, M. de L.** 1995. The breeding biology of the Gadfly Petrels *Pterodroma* spp. of the Pitcairn Islands: characteristics, population sizes and controls. *Biol. J. Linn. Soc.* **56**: 213–231.
- Burger, A.E. & Lawrence, A.D.** 2000. *Seabird Monitoring Handbook for Seychelles*. Mahé: Birdlife Seychelles.
- Burnham, K.P. & Anderson, D.R.** 2002. *Model Selection and Inference: a Practical Information–Theoretic Approach*. 2nd edn. New York: Springer-Verlag.
- Collar, N.J., Crosby, M.J. & Stattersfield, A.J.** 1994. *Birds to Watch 2: the BirdLife International World Checklist of Birds*. Birdlife Conservation Series 4. Cambridge: Birdlife International.
- Croxall, J.P. & Rothery, P.** 1991. Population regulation of seabirds: implications of their demography for conservation. In Perrins, C.M., Lebreton, J.-D. & Hiron, G.J.M. (eds) *Bird Population Studies. Relevance to Conservation and Management*: 272–229. Oxford: Oxford University Press.
- Diamond, A.W.** 1972. Sexual dimorphism in breeding cycles and unequal sex ratio in Magnificent Frigatebirds. *Ibis* **114**: 395–398.
- Diamond, A.W.** 1975a. The biology of Tropicbirds at Aldabra Atoll, Indian Ocean. *Auk* **92**: 16–39.
- Diamond, A.W.** 1975b. Biology and behaviour of Frigatebirds *Fregata* spp. on Aldabra Atoll. *Ibis* **117**: 302–323.
- Diamond, A.W. & Schreiber, E.A.** 2002. Magnificent Frigatebird *Fregata magnificens*. In Poole, A. & Gill, F. (eds) *The Birds of North America*, No. 601. Philadelphia, PA: Academy of Natural Sciences; Washington, DC: American Ornithologists' Union.
- Dorward, D.F.** 1963. The Fairy Tern *Gygis alba* on Ascension Island. *Ibis* **103b**: 365–378.
- Grimm, V., Wyszomirski, T., Aikman, D. & Uchmanski, J.** 1999. Individual-based modelling and ecological theory: synthesis of a workshop. *Ecol. Model* **115**: 275–282.
- Metz, V.G. & Schreiber, E.A.** 2002. Great Frigatebird *Fregata minor*. In Poole, A. & Gill, F. (eds) *The Birds of North America*, No. 681. Philadelphia, PA: Academy of Natural Sciences; Washington, DC: American Ornithologists' Union.
- Mitchell, P.I., Newton, S., Ratcliffe, N. & Dunn, T.** 2004. *Seabird Populations of Britain and Ireland*. London: T. and A. D. Poyser.
- Nelson, J.B.** 1975. The breeding biology of frigatebirds: a comparative review. *Living Bird* **14**: 113–155.
- Orta, J.** 1992. Family Fregatidae (Frigatebirds). In del Hoyo, J., Elliott, A. & Sargatal, J. (eds) *The Handbook of the Birds of the World*, Vol. 1: 362–375. Barcelona: Lynx Edicions.
- Osorno, J.-L.** 1999. Offspring desertion in the Magnificent Frigatebird: are males facing a trade-off between current and future reproduction? *J. Avian Biol.* **30**: 335–341.
- Phillips, N.J.** 1987. The breeding biology of White-tailed Tropicbirds at Cousin Island, Seychelles. *Ibis* **129**: 10–24.
- Prys-Jones, R.P. & Peet, C.** 1980. Breeding periodicity, nesting success and nest site selection among Red-tailed and White-tailed Tropicbirds on Aldabra Atoll. *Ibis* **122**: 76–81.
- Ratcliffe, N.** 1999. Seabirds on Ascension Island. *World Bird-watch* **21**: 16–18.
- Ratcliffe, N., Schmitt, S.A. & Whiffin, M.** 2005. Sink or swim? Viability of a black-tailed godwit population in relation to flooding. *J. App. Ecol.* **82**: 834–843.
- Reville, B.J.** 1983. Numbers of nesting frigatebirds, *Fregata minor* and *F. ariel* on Aldabra Atoll Nature Reserve, Seychelles. *Biol. Cons.* **27**: 59–76.
- Reville, B.J.** 1988. Effects of spacing and synchrony on breeding success in the Great Frigatebird (*Fregata minor*). *Auk* **105**: 252–259.
- Reville, B.J.** 1991. Nest spacing and breeding success in the Lesser Frigatebird (*Fregata ariel*). *Condor* **93**: 555–562.
- Rotella, J.J., Dinsmore, S.J. & Shaffer, T.L.** 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Anim. Biodiv. & Cons.* **27**: 187–204.
- Snow, D.W.** 1965. The breeding of the Red-billed Tropicbird in the Galapagos Islands. *Condor* **67**: 210–214.
- Stonehouse, B. & Stonehouse, S.** 1963. The Frigatebird *Fregata aquila* of Ascension Island. *Ibis* **103b**: 409–422.
- Stonehouse, B.** 1963. The Tropic Birds (Genus *Phaethon*) of Ascension Island. *Ibis* **103b**: 124–161.
- Trivelpiece, W.Z. & Ferraris, J.D.** 1987. Notes on the behavioural ecology of the Magnificent Frigatebird *Fregata magnificens*. *Ibis* **129**: 168–174.
- Weimerskirch, H., Le Corre, M., Jaquemet, S., Potier, M. & Marsac, F.** 2004. Foraging strategy of a top predator in tropical waters: Great Frigatebirds in the Mozambique Channel. *Mar. Ecol. Prog. Ser.* **275**: 297–308.

Received 27 November 2006;  
revision accepted 27 September 2007.

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