

Conservation of the endangered New Zealand fairy tern

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Abstract

The New Zealand fairy tern *Sterna nereis davisae* has only one small population of c.30 individuals and its conservation is a priority. The population was declining prior to the mid 1980s. Management of the three remaining breeding sites was initiated during 1983/84 and intensified from 1991 onwards. We have collated historic data and reviewed the changes in the population since 1991. Our results illustrate that the number of chicks fledged increased since 1991. Fifty-five chicks fledged between 1991/92 and 2002/03. Demographic modelling based on productivity and age-specific survival estimates predicted that the population should increase at c.1.5% per annum. The predicted results from the demographic model contrasted against the observation of a stable resident population. This difference could have resulted from the movement of individuals out of our study area. Demographic modelling also indicated that the population may have continued to decline at a rate of c.1.4% per annum if management was not initiated. Extinction risk within 50 years has decreased from 0.52 to 0.39.

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1. Introduction

In Australia, New Zealand and New Caledonia fairy terns *Sterna nereis* inhabit sheltered coasts on the mainland as well as inshore and offshore islands. Three subspecies have been recognised: *S. n. nereis*, *S. n. exsul* and *S. n. davisae* (Higgins and Davies, 1996). The NZ fairy tern *S. n. davisae* is known to breed at three sites on the North Island of New Zealand (Parrish and Pulham, 1995a; Parrish and Honnor, 1997), while flocks are ob-

served annually at post-breeding sites (Parrish and Pulham, 1995b). These flocks are small in New Zealand because of the small population, in contrast to the Australian fairy terns *S. n. nereis*, which occur in small to large flocks (Higgins and Davies, 1996). The population was estimated to be 28 individuals in 1994 (Parrish and Pulham, 1995b). Based on observations in the New Zealand Fairy Tern Data Base (MS Access, K. Hansen compiler) between 1994 and 2002, the NZ fairy tern population was thought to comprise a minimum of 21–29 individuals.

The persistence of the NZ fairy tern population has been of concern for a number of years due to the low estimates that several authors have made of breeding pairs (see McKenzie and Sibson, 1957; Falla et al., 1979; Shaw, 1985). Furthermore, Bell (1986) classified the NZ fairy tern as endangered and the species is ranked Nationally Critical (a species with a very high

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risk of extinction) (Hitchmough, 2002). The Department of Conservation, New Zealand, has continued intensive ongoing management actions since 1987/88 following the initiation of management by the former New Zealand Wildlife Service during 1983/84 (Parrish and Honnor, 1997). The level of protection was erratic in the early years with little if any monitoring of changes in population and demographic variables (Parrish and Honnor, 1997).

In evaluating the effects of conservation actions on NZ fairy terns, we expected the population to increase and that demographic variables should predict a recovery. Here, we report on the likely impact of conservation actions on the NZ fairy tern population by reviewing historical observations and analysing breeding success, age-specific survival rate and changes in total abundance since intensive management was gradually phased in from 1991 onwards. We also use the information to develop a stochastic demographic model predicting NZ fairy tern abundance for the next 50 years and discuss the implications for NZ fairy tern conservation management.

2. Methods

2.1. Study sites

Since 1983/84, NZ fairy terns have bred at only three sites, Waipu Estuary sand spit, Mangawhai Harbour sand spit and Papakanui sand spit (Parrish and Pulham, 1995b) (Fig. 1). Waipu Estuary is a small estuary located at the mouth of the Waipu River (174°29'E, 36°00'S) with a 3.5 km long, but narrow sand spit. The estuary covers 180 ha with the sand spit (c.100 ha) comprising moderate vegetation cover of low herbaceous and woody plants and stable dunes containing limited breeding areas.

Mangawhai Harbour (174°36'E, 36°06'S) is a dual armed estuary enclosed at times by a broad 3.5 km long sand spit. The entire harbour is around 500 ha in extent with the sand spit comprising c.250 ha. The sand spit is lightly vegetated with extensive bare mobile sand and shell areas.

Papakanui Spit (174°10' E, 36°26'S) is a sand spit 6 km in length and c.150 ha in area enclosing Waionui Inlet. The entire study area comprises c.2400 ha at South Head, and is part of the 95,000 ha Kaipara Harbour. The sand spit is lightly vegetated and has highly mobile dunes.

A number of flocking sites were regularly visited during our study (Fig. 1). Observers visited Te Arai, consisting of a small stream draining from a dune lake system to the coast, during late summer and early autumn. Shortly after breeding some birds gather here before moving to roost sites on the Kaipara Harbour. We vis-

ited known flocking sites on the Kaipara Harbour over autumn and winter. Tauhoa River and Waikiri Creek have extensive areas of mangroves and smaller areas of open sand-mud flats suitable for roosting. Taporā Sand Island is a large sand island on the Kaipara Harbour that has flat, sparsely vegetated, sandy foreshore areas that are also used as roost sites. Immature banded birds were occasionally reported from other locations around the North Island. For instance, in recent years young birds have been sighted at Miranda, on the Firth of Thames, and the Manawatu Estuary.

2.2. Management actions

Conservation management of the NZ fairy tern population has been adapted since it was initiated, with the amount of effort and manipulations generally increasing over the study period. Management actions include full-time wardens employed over the breeding season; trapping to remove introduced mammalian predators during the breeding season and control of aerial predators; temporary fencing around nesting areas to reduce disturbance and trampling of nests by people; nest protection against weather events, e.g., sand-bagging nests from tidal surges; ditch and dyke systems to protect low-lying nests from high tides; nest manipulations including moving abandoned or threatened eggs or chicks between recipient nests in the wild or to temporary captivity; advocacy of the endangered status of NZ fairy tern and their habitat; compliance enforcement of the legislation governing the NZ fairy tern breeding habitat by public beach users (Parrish and Honnor, 1997).

Initial monitoring and management, from 1983/84 until 1990, was erratic with inconsistent coverage at the breeding sites and wardens employed for only a maximum of two months at any one site (Fig. 2). Between 1991 and 1995 the monitoring effort was increased to three to four months per site. By 1998, all three sites were monitored for at least five months each breeding season.

Ground-based predator control was started at Mangawhai in 1995 and Waipu in 1997 for five months of the breeding season. Predator control at Papakanui also started in 1997, but only for two months for the first two years. By 1999 all three sites each had a full-time warden and trapper for at least five months over the breeding season.

Trapping precedes monitoring each breeding season by approximately one month. Control of aerial predators was carried out as required. A large colony of black-backed gulls (*Larus dominicanus*) was poisoned at Mangawhai in 1997 and since then adults have been discouraged from nesting at all three sites by pricking or destroying eggs. Australasian harriers (*Circus approximans*) were destroyed when identified as posing a threat to nesting NZ fairy terns.

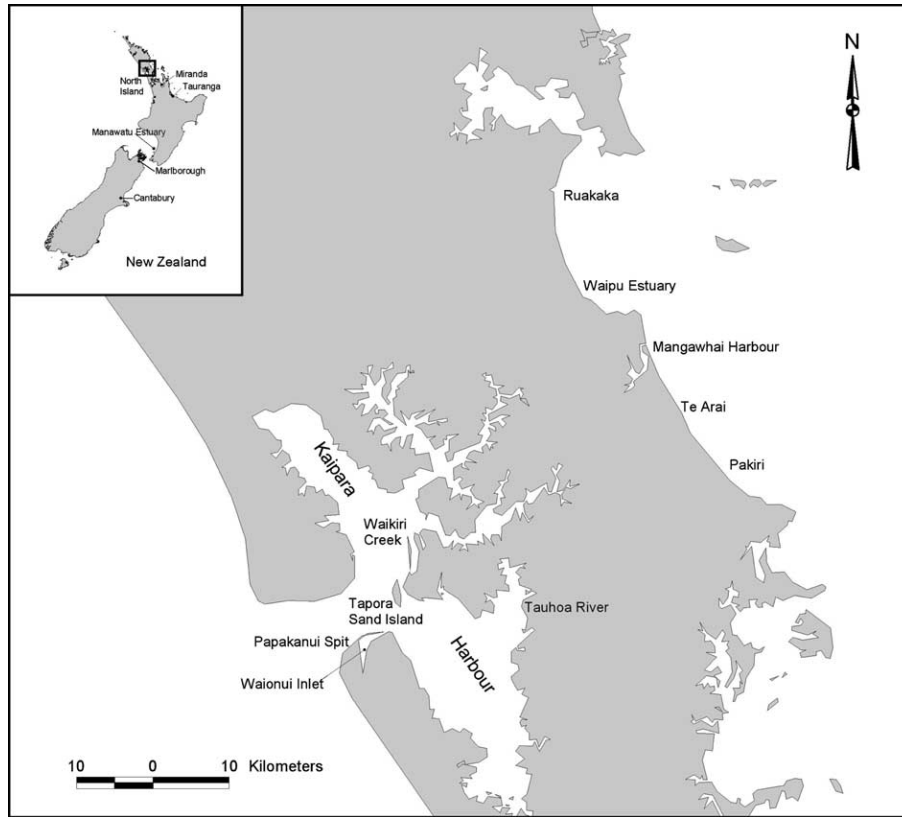


Fig. 1. Breeding localities and post-breeding flocking sites of New Zealand fairy terns on the North Island of New Zealand.

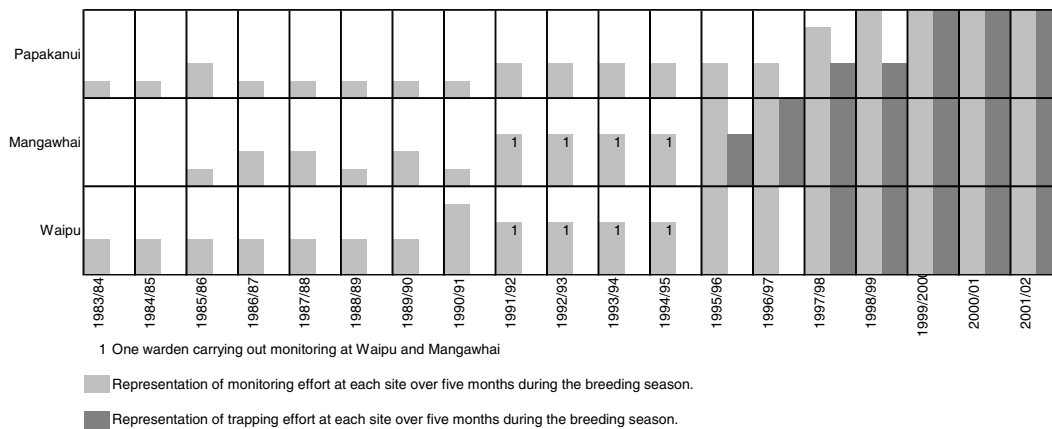


Fig. 2. Schematic illustration of the monitoring and trapping effort at three key breeding areas during the study period from 1983 to 2002. We present management effort completed over five months in summer every year. A complete bar represents effort for all five months with other effort shown proportionally.

Captive facilities were used in 1986/87, 1992/93 and 1996/97, on an ad hoc basis (Parrish and Honnor, 1997), and each year since then. From 1998 onwards protocols for taking abandoned eggs into temporary captivity and their return to the wild were developed and the arrangement formalised with Auckland Zoological Park.

2.3. Breeding

From 1991 to 2002, wardens were employed each breeding season to monitor breeding attempts. Once detected nests were observed regularly and usually on a daily basis. Nests were checked for presence of an incubating adult and incubating behaviour, e.g., female fed

on the nest or change-over of incubating male and female. If weather conditions were deteriorating or problems with incubating adults were detected then observations were carried out over several hours and protection measures taken if needed. Once the number of eggs in the nest was determined and recorded, the nest was observed from a minimum distance of 50 m with a spotting scope so that incubating birds were not disturbed. Each nest was generally visited three times during incubation (c.22 days of incubation during October–January) to determine the number of eggs it contained, to determine fertility by candling and finally once the chick(s) had hatched. The fledging period is c.23 days (Parrish and Pulham, 1995a). The number of chicks hatched and fledged per nest was recorded. Chicks were also observed regularly, from a distance of at least 80 m, to determine their presence, presence of a guarding parent and that the chicks were being fed. Chicks were observed for the following four weeks until they had fledged and over the next few weeks to two months until they moved from their natal site to a flocking site.

We collated values for the Southern Oscillation Index, a measure of change in the atmospheric pressures across the Pacific Ocean (National Institute of Water and Atmospheric Research, 2002), as a measure of adverse weather. The frequency of storms during a season increases as the Southern Oscillation Index increases, i.e., moves from El Niño to La Niña (National Institute of Water and Atmospheric Research, 2002). We predicted that as the probability of increased incidences of major storm events increased (i.e., an increase of Southern Oscillation Index values), hatching rates should decline because storm events result in tidal surges flooding nests and/or wind blown sand either covering nests or forcing adults to abandon nests (K. Hansen, R. Parrish, G. Pulham, pers. obs.). Reproductive variables; number of breeding pairs, number of chicks fledged, clutch size, hatching and fledging proportions were related through regression analysis to the Southern Oscillation Index to evaluate the effects of weather on NZ fairy tern productivity.

2.4. Survival

Chicks ($n = 55$) were colour-banded a few days prior to fledging and estimates of age-specific survival obtained. Each chick was banded with a size C, numbered metal band on one tarsus and one or two colour bands on the other tarsus. During the 1990/91 and 1991/92 seasons, size B wrap-around colour bands were used, but replaced subsequently by size C (end-butting) colour bands. The latter bands allowed up to two colour bands to be placed on the tarsus without a metal band.

Banding combinations were recorded whenever opportunities presented themselves, whether it was during breeding, post-breeding or winter months. From

these re-sighting records a “capture” history on an annual basis was generated for each individual, and these ‘band re-sightings’ used for age-specific survival analyses. Age-specific survival estimates were calculated using MARK (White and Burnham, 1999). Our analyses focused on estimating survival rates of fledging to adulthood and annual adult survival. Our data did not allow us to check for differences in encounter rates between the 12 years of observations.

2.5. Estimation of population size

NZ fairy terns were observed for n occasions during March and April of each year. On each occasion, the total number of birds sighted, the colour-band combinations identified and the number of unbanded birds were recorded. We used CAPTURE (White et al., 1978) to obtain estimates of population size for each post-breeding season for 1993–2002. No suitable observations were recorded during 1991 and 1992. Our low sample size of marked individuals forced the use of the CAPTURE Null Model assuming equal encounter rates.

2.6. Demographic population model

We developed a simple age-structured, birth-pulse, post-breeding population model using a Leslie Matrix definition as follows:

$$\begin{bmatrix} N_{c,t+1} \\ N_{sa,t+1} \\ N_{a,t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & s_a \tau \zeta \varphi (p_1 + p_2 + p_3) \\ s_c & 0 & 0 \\ 0 & s_{sa} & s_a \end{bmatrix} \times \begin{bmatrix} N_{c,t} \\ N_{sa,t} \\ N_{a,t} \end{bmatrix} \quad (1)$$

where $N_{c,t}$, $N_{sa,t}$ and $N_{a,t}$ are the number of chicks, fledglings and adults at time t , respectively. Age-specific survival rates are represented by s_c (chick survival from hatching to fledging), s_{sa} (fledging survival from fledging to adult) and s_a (adult survival rate annually). Fecundity is defined by the equation $\tau \zeta \varphi (p_1 + p_2 + p_3)$ and included in the model (1), where τ represents sex ratio of chicks, ζ represents clutch size, φ the proportion of eggs hatching and p_1 , p_2 and p_3 the proportion of adults attempting to breed 1, 2 or 3 times during a season.

The small population necessitated the removal of demographic variance from total variance (Kendall, 1998; Akçakaya, 2002; White et al., 2002). We removed demographic variance for survival and fecundity estimates using Akçakaya (2002) approach before allowing 10,000 model iterations to derive predictions for 50 years. For each model repeat, survival and fecundity estimates were drawn from the normal distributions defined by respective averages and corrected variances. We derived lambda (λ) as a finite population growth rate from the dominant eigenvalue of the Leslie Matrix

(Caswell, 2000) and converted these to exponential growth rates as $\ln(\lambda)$. Exponential population growth and confidence intervals were derived from all model iterations. Extinction risk was calculated as the proportional frequency of iterations that predicted populations smaller than three individuals after 50 years.

No demographic estimates were available prior to 1991. In addition, our sample size is too small to calculate demographic estimates independently for each year since 1991, when management gradually improved. To evaluate what the likely effect of management was, we made an informed assessment. Management is completely focussed on improving breeding outputs. We therefore expected that hatching rate and chick survival were the variables most improved due to management. The Leslie matrix was reconstructed by halving these two variables. Improvements in hatching rate and chick survival were the likely effects expected by the New Zealand Fairy Tern Recovery Group (Parrish and Honnor, 1997). We used these as hypotheses and calculated population growth rate and extinction risk as before, to evaluate the most likely effect of management.

3. Results

3.1. Historic observations of NZ fairy terns

Prior to the 1950s, observations of NZ fairy terns were haphazard and individual fairy terns often confused with little terns *S. albifrons* (McKenzie and Sibson, 1957; Sibson and Edgar, 1962). Nonetheless, records collated from the NZ Fairy Tern Database, suggest that NZ fairy terns were at least recognised and regularly sighted in New Zealand. From the 1950s onwards, regular visits to various localities resulted in the only reliable long-term counts. The highest numbers were recorded during the mid 1970s followed by a marked decline. Our analysis showed that the population declined at an exponential rate of -0.085 ± 0.012 ($\bar{x} \pm \text{SE}$, $n = 18$ years, $F_{1,16} = 48.92$, $P < 0.01$, slope of a linear regression analyses of $\ln(N)$ over time where N is the population size) per annum until 1991 (Fig. 3(a)). However, during the same period (1975–1991) the number of known breeding pairs in the total population did not show a declining trend even though the number of pairs fluctuated between two and five (Fig. 3(b)).

3.2. Recent records of NZ fairy terns

Since 1991, observations of NZ fairy terns have been more precise and regular, due to the presence of banded individuals in the population and the increased management effort by a variety of organisations, particularly the New Zealand Department of Conservation and the Ornithological Society of New Zealand. The numbers

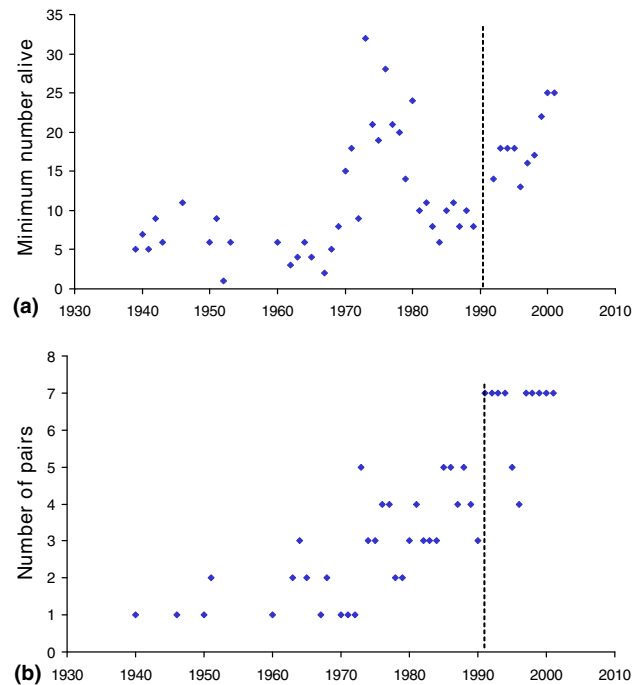


Fig. 3. Historic records of New Zealand fairy terns. (a) Minimum number of fairy terns known to be alive. The data prior to the 1950s is constrained by potential mis-identification. Since the 1970s numbers declined, but increased following the initiation of intensive management during 1991 (vertical broken line). (b) Number of known fairy tern pairs nesting, which appear to increase over time.

of birds appear to have increased at an exponential rate of 0.052 ± 0.018 from 1991 to 2001 ($n = 10$ years) which was significantly different from zero ($F_{1,8} = 8.10$, $P < 0.01$, linear regression analyses of $\ln(N)$ over time where N is the population size) (Fig. 3(a)). The number of pairs from 1991 onwards was also higher than before improved management was initiated in 1991 ($t_{30} = 7.29$, $P < 0.01$, t -test) (Fig. 3(b)).

3.3. NZ Fairy Tern breeding since 1991

The proportion of all adults breeding differed between breeding seasons with a lower proportion breeding during the 1995/96 and 1996/97 seasons than during any other season (t_s -tests) (Fig. 4). However, excluding 1995/96 and 1996/97, we conclude that little temporal trends in adult breeding proportion exist. Combining all adults breeding once a season since 1991 resulted in 43% (0.43 ± 0.09 , $n = 122$) of the total adult population attempting to breed during any particular breeding season. On average $16.97 \pm 4.68\%$ ($n = 122$) of the adult population attempted to breed only once during a breeding season, $21.21 \pm 11.64\%$ ($n = 122$) attempted to breed twice, and $2.66 \pm 1.31\%$ ($n = 122$) attempted to breed three times. A higher proportion of adults attempted to breed twice during 1993/94 than during any other breeding season, while some individuals attempted to breed three times during

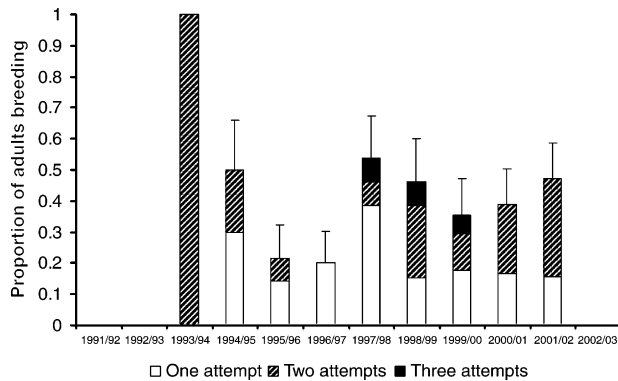


Fig. 4. Relative frequency of banded adults recorded as attempting to breed. Note that 2nd or 3rd breeding attempts were a result of the preceding nesting attempt failing.

1997/98, 1998/99 and 1999/00 (Fig. 4). Note that all multiple breeding attempts were re-nestings, after the previous nest had failed during a particular breeding season.

Since 1991, clutch size has not changed significantly between breeding seasons (ANOVA, $F_{11,120} = 0.82$, $P = 0.62$) (Table 1). The combined results of all the breeding seasons gave a clutch size of 1.67 ± 0.04 ($n = 120$) for NZ fairy terns during our study. Hatching proportion appeared to be high during 1991/92 (Table 1), but the variation recorded between years resulted in no overall significant differences between breeding seasons (ANOVA, $F_{11,120} = 0.62$, $P = 0.81$). The combined hatching proportion was estimated as 0.38 ± 0.04 ($n = 121$). In contrast, fledging proportion differed significantly between breeding seasons. This was as a result of no chicks fledging during the 1996/97 season, which was significantly different from the higher fledging rates recorded in all the other years since 1991 (ANOVA, $F_{11,55} = 2.02$, $P = 0.05$, post hoc Tuckey multiple range tests) (Table 1). Excluding 1996/97, fledging proportion did not change (ANOVA, $F_{10,53} = 1.55$,

$P = 0.56$) between 1991/92 and 2002/03 and was recorded as 0.74 ± 0.06 ($n = 54$).

A variable number of fledglings were produced each breeding season with the most in 2001/02 (8 chicks) and none in 1996/97 (Table 1). On average 5.33 ± 0.82 fledglings were produced per breeding season ($n = 12$). No significant relationships were recorded between the number of fledglings produced in a given year and the numbers produced one year later (Linear Regression Analysis, $F_{1,9} = 0.19$, $P = 0.67$), or two years later (Linear Regression Analysis, $F_{1,8} = 0.51$, $P = 0.49$).

The number of breeding pairs (Linear Regression Analysis, $F_{1,21} = 0.23$, $P = 0.63$), total number of chicks fledged (Linear Regression Analysis, $F_{1,17} = 0.31$, $P = 0.58$), clutch size (Linear Regression Analysis, $F_{1,10} = 0.08$, $P = 0.78$), hatching proportion (Linear Regression Analysis, $F_{1,10} = 1.37$, $P = 0.27$) and fledging proportion (Linear Regression Analysis, $F_{1,10} = 0.19$, $P = 0.67$) were not associated with the Southern Oscillation Index. Neither the number of breeding pairs (Linear Regression Analysis, $F_{1,8} = 0.02$, $P = 0.88$), total number of chicks fledged (Linear Regression Analysis, $F_{1,8} = 1.77$, $P = 0.22$), clutch size (Linear Regression Analysis, $F_{1,8} = 2.19$, $P = 0.12$), hatching proportion (Linear Regression Analysis, $F_{1,8} = 1.35$, $P = 0.28$) or fledging proportion (Linear Regression Analysis, $F_{1,8} = 0.04$, $P = 0.85$) were associated with population size.

3.4. Age-specific life-history variables

It was estimated that 63% of fledglings survive per annum until they reach adulthood (0.63 ± 0.05 , $n = 55$), while 95% of adults survive each year (0.95 ± 0.02 , $n = 30$). Assuming that these rates remain relatively constant, a life expectancy at fledging of six years is predicted for NZ fairy terns in the study area. It is noteworthy that 13 banded-individuals were not recorded for 1–5 consecutive years in New Zealand. Three

Table 1

Breeding variables (mean \pm SE) recorded for New Zealand fairy terns since intensive management was initiated during 1991

Year	Clutch size	Proportion hatched	Proportion fledged	Fledglings	Nests
1991/92	1.83 \pm 0.17	0.67 \pm 0.21	0.80 \pm 0.20	6	7
1992/93	1.88 \pm 0.13	0.38 \pm 0.16	0.88 \pm 0.13	5	8
1993/94	1.45 \pm 0.16	0.32 \pm 0.12	0.40 \pm 0.24	3	11
1994/95	1.77 \pm 0.12	0.31 \pm 0.12	0.40 \pm 0.24	2	13
1995/96	1.75 \pm 0.16	0.38 \pm 0.18	1.00 \pm 0.00	6	8
1996/97	1.60 \pm 0.24	0.30 \pm 0.20	0.00	0	5
1997/98	1.54 \pm 0.14	0.46 \pm 0.13	0.57 \pm 0.20	7	13
1998/99	1.75 \pm 0.13	0.29 \pm 0.11	0.80 \pm 0.20	5	12
1999/00	1.75 \pm 0.13	0.42 \pm 0.12	0.64 \pm 0.18	7	12
2000/01	1.64 \pm 0.15	0.55 \pm 0.16	1.00 \pm 0.00	4	10
2001/02	1.50 \pm 0.14	0.29 \pm 0.11	1.00 \pm 0.00	8	14
2002/03	1.75 \pm 0.16	0.25 \pm 0.16	1.00 \pm 0.00	2	8

None of the variables changed over time with the exception of the proportion fledging during 1996/97, which was significantly lower than the proportions fledging during other years.

banded-individuals were not recorded for five consecutive years, two individuals were not recorded for four years, one individual was not recorded for three years, one for two years, and six banded-individuals were not recorded for one year.

Eighteen individuals that were banded as chicks have been recorded breeding. The individuals from cohorts banded during 1990/91 and 1991/92 first attempted to breed at 2.50 ± 0.55 ($n = 6$) years of age. Individuals of cohorts banded between 1992/93 and 1997/98 attempted to breed for the first time at significantly older ages at the 10% confidence level (3.50 ± 1.41 years, $n = 8$) (t -test, $t_{12} = -1.63$, $P = 0.07$). However, since 1998/99 individuals of cohorts have attempted to breed at 2.25 ± 0.96 years ($n = 4$) after banding.

3.5. Population size and model predictions

Population estimates from 1993 onwards ranged from 18 in 1993 to 35 in 2000 and 2001 (Table 2). Over the same period, the number of breeding pairs varied between four and seven. Predictions derived from the age-specific demographic model illustrated that the NZ fairy tern population should be increasing at an exponential rate of 0.015 ± 0.009 (average \pm SE, $n = 10,000$) under the present demographic and management scenario (Fig. 5). Estimates of population size from band re-sightings were higher than those predicted from the demography of the population prior to 1999 and lower from 1999 onwards (Fig. 5). Nonetheless, our model predicted that the population still suffers a 0.39 ± 0.01 (average \pm SE, $n = 10,000$) probability of going extinct in 50 years time.

If management was withdrawn, the proportion of eggs hatching is expected to drop to 19% with only 37% of those fledging. Our demographic model predicts a population decline at an exponential rate of -0.014 ± 0.002 ($n = 10,000$) where the population would have a 0.52 ± 0.01 ($n = 10,000$) probability of going extinct in 50 years.

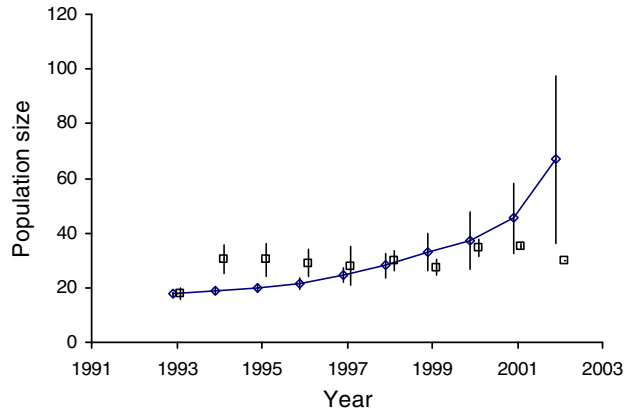


Fig. 5. Estimates of population sizes predicted from demographic variables (◆) recorded for New Zealand fairy terns during the present study. It is predicted that the population should be increasing at an exponential rate of 0.015 per annum. Comparison between demographically estimated population predictions and population estimates from band re-sights (□) during 1993–2002 suggest that demographic prediction were higher after 1999.

4. Discussion

Our review of historic observations suggests that NZ fairy terns were not overly common in New Zealand. This is in contrast to Buller (1888) who described NZ fairy terns as “tolerably common”, while Oliver (1955) believed that NZ fairy terns were common in Marlborough and Canterbury (Fig. 1). Early historical observations often recorded little terns as NZ fairy terns (McKenzie and Sibson, 1957; Sibson and Edgar, 1962). We therefore believe that the NZ fairy tern population was never characterised by high numbers, even though there were records of breeding birds at Tauranga, Pakiri, Te Arai, Ruakaka, Papakanui Spit, Mangawhai, Tabora and Waipu between 1940 and 1983 (Fig. 1). During the late 1980s and into the 2000s (1984–2002), breeding was recorded only at Papakanui Spit, Mangawhai and Waipu (Parrish and Pulham, 1995b;

Table 2
Population sizes estimated for New Zealand fairy terns using band re-sights since 1993

Year	N	SE	Sightings	Minimum number of banded birds present	% of sightings without bands
1993	18	0.66	44	8	20.89
1994	30	1.47	75	12	47.44
1995	30	1.55	69	12	46.47
1996	29	1.10	124	18	39.30
1997	28	1.75	93	13	52.50
1998	30	0.78	164	17	31.41
1999	27	0.65	75	15	26.67
2000	35	0.60	83	22	21.52
2001	35	0.19	97	25	16.86
2002	30	0.01	64	25	10.71

The estimate-precision increased as the number of banded birds in the population increased.

Parrish and Honnor, 1997; K. Hansen, R. Parrish, G. Pulham, pers. obs.).

From the 1950s, reliable identifications resulted in more accurate estimates of total numbers of NZ fairy terns. These more recent observations clearly illustrated that from mid 1970s to 1980s NZ fairy tern populations declined at an exponential rate of nearly 10% per annum. The decline was substantially slowed during the period of management initiated by the New Zealand Wildlife Service in 1983. These data together with estimates of NZ fairy tern numbers after 1991 could illustrate fluctuations that may suggest a natural oscillation that happens to coincide with the onset of management. Analysis of responses to future management will determine if this is the case.

During the same time the number of pairs did not show similar trends. In fact, it would appear that the number of pairs increased from the 1970s to the end of the 1980s irrespective of management initiated by the New Zealand Wildlife Service. In the mid-1990s, the number of pairs reached a plateau at seven, which may only reflect incomplete sampling during the 1970–1980s. Nonetheless, at any one site only 1–3 pairs were present. As only a proportion of the adults was breeding, it could be expected that breeding adults were progressively dying, probably of old age, and being replaced by existing non-breeding adults. It is likely that recruitment of chicks into the adult breeding population was insufficient to maintain the population.

Management during the late 1980s was directed at improving the survival of chicks. Parrish and Pulham (1995b) recorded that only 18 chicks fledged between 1947 and 1983, although the actual number is likely to be higher. In contrast, at least 22 chicks fledged between 1983 and 1990 as a result of actions taken during that time. This was most likely the factor that slowed down the population decline, but it was not stopped. The Department of Conservation progressively intensified its management programmes from 1991 onwards by initiating research, reinstating wardens at all the breeding sites and introducing video-monitoring at selected nests. However, it was not until 1995/96 and 1997/98 that the full suite of management actions was implemented at Mangawhai, Waipu and Papakanui. Management included predator control, advocacy, manipulation of nests that were threatened or abandoned and banding of all chicks.

Our population estimates from banded individuals suggest that the population size of NZ fairy terns stayed stable during our study period (1991–2002), with the population estimated at 30 individuals in 2002. This was similar to Parrish and Pulham (1995b) count (28) during 1994. Our estimate was surprising considering management effort over the last decade. Perhaps management did not improve the chance of persistence for NZ fairy terns. Several addi-

tional explanations are also possible. First, it is likely that Parrish and Pulham (1995b) over-estimated the population size, since we would have expected the 2002 population to be much larger based on productivity over the last decade. However, it is more likely that management was effective in protecting adults and their breeding attempts, but that increases in the population were not observed because individuals moved out of our study area. Let us consider the demographic results obtained in the present study.

We have shown an apparent increase in the absolute number of fledglings produced per breeding season since the intensified management started during 1991/92. Parrish and Pulham (1995b) recorded 3.13 ± 0.52 ($n = 8$) fledglings per breeding season from 1983 to 1990. Even though the number of fledglings produced per breeding season since 1991 was not significantly more than before (5.33 ± 0.82 , $n = 12$, t -test, $t_{19} = -1.13$, $P = 0.14$), nearly double the number of fledglings were produced from the 12 years after 1991 (64 fledglings) compared to the 12 years before (38 fledglings). In reality 28 were produced in eight years before intensified management, while 64 came from 12 years of management. For small populations such contributions can have enormous effects on reducing extinction risks. Clutch size, hatching proportion and fledging proportion did not differ significantly between breeding seasons although substantial variation existed between pairs within a particular breeding season. We did not expect clutch size to vary and this was confirmed by our data.

We believe that external factors contribute substantially to the outcome of nests. No density-dependence of fledgling numbers was recorded, suggesting that inherent population mechanisms do not play a major role in fledgling success of NZ fairy terns. The variation in hatching rate was not associated with an index of adverse weather, the Southern Oscillation Index (National Institute of Water and Atmospheric Research, 2002). Note that we have not explicitly investigated the potential consequences of the influence of the Southern Oscillation Index on food availability. Lyver et al. (1999) recorded that varying sea-surface temperatures influenced sooty shearwater *Puffinus griseus* chick production, through potentially affecting food availability. This mechanism of Southern Oscillation Index influence is unlikely for NZ fairy terns because none of the other components of productivity that may be associated with food availability (number of eggs and fledging proportion) were associated with the Southern Oscillation Index. We therefore believe that most nest failures were associated with random processes since the onset of intensified management since 1991. Most other factors have been accounted for and minimised by the present management regime of predator control and public advocacy. Recently, management actions such as translocation of eggs between nests or temporarily into

captivity have most likely reduced risks associated with weather conditions.

The low hatching rate of 38% is of concern. The intensified management has probably minimised most external effects (human disturbance, predators and random weather events) on hatching rate. However, a number of infertile eggs ($n = 33$, Parrish and Honnor, 1997; K. Hansen, pers. obs.) were recorded during the study period. If management actions directed at minimising external effects have reached their ceiling, inherent effects such as inbreeding depression may be more significant for the NZ fairy tern population in the long-term.

The production of fledglings is not the only population variable that affects population change. Our observations indicated that NZ fairy terns have the potential to breed during the second breeding season following hatching and we assumed that adulthood is reached at two years of age. Our analysis illustrated that c.63% of fledglings survived the first year and c.95% the second year following hatching. This resulted in at least 60% of fledglings being recruited into the adult population. No similar measurements were made prior to 1990, but we can assume that survival rates would have been approximately similar because no management actions were specifically targeted at post-fledging stages of the life history of NZ fairy terns.

In our analysis, adult survival rate was 95% per annum. The combined effects of these age-specific survival rates are that life expectancy at hatching will be >6 years. Between 1992 and 1998 a higher proportion of individuals started breeding later in life than before 1992. In addition, only a proportion of the adults attempted to breed during the study period. For example, less than 20% of the adult population attempted to breed during 1995/96 and 1996/97, while more than 80% attempted to breed during 1997/98 and 1998/99. An overall average of 43% of the adults has attempted to breed during any particular breeding season since 1991. We are unsure of the reasons for this. We speculated that this may be a result of limitations in the breeding areas, as the quality of habitat in the current breeding locations fluctuates from season to season. For instance, wind shifts sand dunes to cover and uncover areas of shell during and between breeding seasons. However, as we found no evidence for density dependence it is unlikely that breeding habitat is limited at the current population size.

We are also unable to explain why age at first breeding apparently increased between 1992 and 1998. This could simply reflect normal demographic fluctuation. When intensive management started in 1991, most breeding adults were old with few non-breeding adults around to replace them. The successes of nests, as a result of the management, produced new adults, which were immediately recruited into the breeding adult population. It appears that during the latter part of the

study, fledglings recruited into the adult population have waited to breed, or have emigrated from our study sites. We have a number of records where individual NZ fairy terns have not been recorded for up to five seasons at our study sites, before finally re-appearing and successfully breeding. Some NZ fairy terns may leave New Zealand for extended periods, although no sightings of banded birds have been reported from elsewhere. We have no idea where they go or whether they are interacting reproductively with the other two fairy tern sub-species.

Pairs that were breeding during the latter part of the study were attempting to breed repeatedly up to three times during a season, when a nest was lost or abandoned for some or other reason. This may compensate for failed nesting attempts and/or the proportion of adults not breeding. However, the low incidence of multiple breeding attempts will only have a small impact on total fledgling production.

Our analyses have illustrated that the production of fledglings improved during the period of intensive management actions. We cannot unequivocally assign this to the management actions, but more fledglings certainly contributed to the conservation of NZ fairy terns since 1991. We have also illustrated that sub-adult and adult survival rates are reasonable, but that only a proportion of adults breeds every breeding season.

What does this mean for NZ fairy tern in the long-term? Our population model, using the demographic variables obtained, predicts an increase of 1.5% per annum. We have no evidence of density-associated factors that impact on demographic variables. Our demographic predictions were higher than those estimated from band re-sightings during the latter part of the study. The band re-sightings recorded the population fluctuating between 18 and 32 individuals from 1992 to 2002. Estimates of the population from band re-sights represent the population of resident birds as defined by our method of estimation. Considering that we have recorded individuals absent from our New Zealand study sites, it was not surprising to record a difference between demographic predictions and band re-sight estimates.

What would most likely have happened if no management actions were undertaken? Our model predicts that the population would have declined at a rate of c.1.4% per annum. We therefore believe that conservation management actions have most likely contributed substantially to successfully stop the decline in NZ fairy terns. Our models predict that population extinction risk was reduced from c.52% to c.39%. However, the population is still in a precarious position because it is vulnerable to unpredictable population events and it is evident that management actions directed at maintaining fledgling production are vital to maintaining the present NZ fairy tern population. The population is extremely

vulnerable to stochastic effects and inbreeding depression due to its small size (Soulé, 1987). Conservation managers could potentially deal with the stochastic risk by increasing the population size through measures other than those already in place, such as successful captive breeding. We realise that management directed at the juvenile stages is probably at the extreme, but our model indicates that getting a higher proportion of adults to breed will result in substantial increases in the population. There is a critical need for further research to understand the dynamics of breeding and factors influencing these.

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