

Short Communication

New Zealand endemic open-habitat specialist, the Black-fronted Tern (*Chlidonias albostratus*), experienced population expansion during Pleistocene glaciation and recent decline

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Understanding how climatic and environmental changes, as well as human activities, induce changes in the distribution and population size of avian species refines our ability to predict future impacts on threatened species. Using multilocus genetic data, we show that the population of a threatened New Zealand endemic open-habitat specialist, the Black-fronted Tern *Chlidonias albostratus* – in contrast to forest specialists – expanded during the last glacial period. The population has decreased subsequently despite the availability of extensive open habitat after human arrival to New Zealand. We conclude that population changes for open habitat specialists such as Black-fronted Terns in pre-human New Zealand were habitat-dependent, similar to Northern Hemisphere cold-adapted species, whereas post-human settlement populations were constrained by predators independent of habitat availability, similar to other island endemic species.

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Keywords: anthropogenic, birds, climate, demographic history, environmental modification, past population size.

Climatic and environmental changes, as well as human activities, can all induce changes in the distribution and population size of avian species (Waters *et al.* 2017). Some species benefit from expanded suitable habitat, whereas others decline and face potential population bottlenecks or extinction (Clucas *et al.* 2015, Zhen Tan *et al.* 2021). In New Zealand (NZ), the extinction rates of birds have been among the highest globally: with c. 80 of 230 lineages having become extinct since human settlement (Holdaway 1999, Brooks *et al.* 2002). While predation by introduced mammals is the primary cause of extinction (Innes *et al.* 2010), climate change and habitat availability have also been suggested to be important drivers of changes in population size through time (Nadachowska-Brzyska *et al.* 2015). Using molecular techniques, it is possible to assess demographic history and better assess vulnerability of a species to global change.

For many species, Quaternary glacial periods had differing effects on the large continental landmasses in the Northern Hemisphere compared with the predominantly oceanic island systems in the Southern Hemisphere (Fraser *et al.* 2012). In the Northern Hemisphere, large areas of land at higher latitudes were covered periodically by expanding glaciers (Hewitt 2004). In contrast, glaciation was comparatively limited in the Southern Hemisphere, resulting in the expansion of open, non-forest ecosystems (Hope *et al.* 2004, Lorrey & Bostock 2017). NZ is an exemplary system for understanding Southern Hemisphere biogeography and also the effects of human modifications to the environment (Wallis & Trewick 2009).

During the last glacial period (73 000–14 000 years ago), terrestrial land area, including river braid plains, expanded with globally lowered sea levels and NZ's coastline extended beyond its present-day limits by c. 70 km (Browne & Naish 2003). The expanded lowland areas, particularly around the modern-day South Island/Te Waipounamu, were dominated by dry grasslands with some shrubs and small forest pockets (Newnham *et al.* 2013, Mortimer *et al.* 2017). As the climate warmed in the Holocene, closed-canopy forests expanded and covered 85–90% of NZ (McGlone 1989).

In more recent times, humans – accidentally or intentionally – have been a main driver of environmental change. Polynesian settlers first arrived in NZ in the 13th century, followed by a wave of European colonization beginning in the 19th century (Wilmshurst *et al.* 2008). Within 200 years of Polynesian settlement, humans had burned nearly 50% of the forest with a further 25% of forest burned or clear-felled briefly after the

second wave of immigration (McWethy *et al.* 2014). Today, forest covers only *c.* 25% of NZ's land surface and there is little forest cover, particularly in the dry eastern areas of the South Island (Perry *et al.* 2014). While worldwide loss of forest cover has devastating effects for populations of forest-dwelling species (Hansen *et al.* 2010, Hedges *et al.* 2018), it could be potentially beneficial for open-habitat specialists. However, other anthropogenic impacts and environmental modifications to NZ also include the introduction of exotic fauna and flora (King 1984). Alien, predatory mammals have had particular devastating effects on NZ's native avifauna (Sanders & Maloney 2002, Innes *et al.* 2010). Many extant native species are still vulnerable to predation and habitat loss, and have declined significantly (Robertson *et al.* 2021).

Globally, populations of open-habitat specialists expanded ranges as they benefitted from vegetation change during glacial periods (Kearns *et al.* 2014). Research on past population changes of NZ's avifauna has focused on forest and alpine species, and has generally followed a refugia paradigm of populations expanding after the last glacial maximum (e.g. Grosser *et al.* 2017). However, a unique guild of birds, including the endemic Black-fronted Tern (Māori: Tarapirohe) *Chlidonias albostratus*, are open habitat specialists (Schlesselmann *et al.* 2017, Hamblin *et al.* 2019). They breed on bare gravel areas in rivers and even establish breeding colonies at high altitude (*c.* 1720 m asl; Child 1986). Black-fronted Terns forage for fish, invertebrates and lizards over freshwater and open grass- or shrubland (Lalas 1977, O'Donnell & Hoare 2009). They are classified internationally as 'Endangered' (BirdLife International 2016) and populations are currently in decline (O'Donnell & Hoare 2011).

Using multilocus genetic data to reconstruct past demography, we tested the following hypotheses.

- In the absence of population limitations induced by novel predators, Black-fronted Terns are habitat-constrained and therefore would have experienced a population expansion during the last glacial period due to favourable habitat conditions analogous to Northern Hemisphere cold-tolerant and Australian arid-tolerant biota.
- Despite open habitat expansion associated with human deforestation, a severe reduction has been experienced due to introduced mammalian predators.

METHODS

Blood samples of 589 Black-fronted Terns were collected from throughout their breeding range and genotyped at 17 microsatellite loci (Schlesselmann & Robertson 2017). Samples that failed to PCR-amplify at

more than one locus were discarded, leaving 422 individuals. For 36 individuals, 1143 base pairs (bp) of the cytochrome B (cytB) gene (mitochondrial DNA (mtDNA)) were determined. For 64 individuals, 898 bp of the mtDNA control region (CR) were sequenced. Descriptions of DNA extraction, sequencing, genotyping procedures and details of samples used are provided in the Supporting Information. We analysed samples from the entire breeding range together, as prior analysis revealed a lack of substructure (Schlesselmann *et al.* 2020; $K = 1$, $F_{ST} = 0.009$). There is considerable uncertainty about the generation time for Black-fronted Terns. Therefore, we present a range of values based on published estimates for other tern species and calculations based on life-history attributes: 5.28 years (Bird *et al.* 2020, Supporting Information Table S4), 9.33 years (IUCN 2022), 10 years (O'Donnell & Hoare 2011; see Supporting Information for further detail).

Neutrality statistics, sequence mismatch analysis and haplotype networks

We examined population fluctuations based on mtDNA by combining sequences excluding individuals with missing data ($n = 27$). We first calculated Tajima's D and Fu's F_S statistics (Tajima 1989, Fu 1997). Negative values of these statistics indicate population expansion, whereas positive values suggest a reduction in population size. Next, we conducted mismatch analyses (MMAs) by generating mismatch distributions. The shape of the distribution is expected to be unimodal in populations that have undergone recent population expansion, and ragged or multimodal when the population has been more stable over time (Rogers & Harpending 1992). We tested the goodness of fit to the expected model of sudden population expansion using the sum of squared deviations (SSDs) and raggedness indices. All analyses were performed in Arlequin v. 3.5.2.2 (Excoffier & Lischer 2010) with 1000 permutations. Last, we investigated evolutionary relationships between haplotypes with median joining networks using PopArt (Leigh & Bryant 2015).

Coalescent analysis

We used an Extended Bayesian Skyline Plot (EBSP) in BEAST v. 2.4.8 to investigate changes in population size through time (Bouckaert *et al.* 2014). We concatenated cytB and CR data ($n = 73$; Supporting Information Table S1). We evaluated the accuracy of the EBSP in detecting demographic expansion by testing an alternative scenario of constant population size (see Supporting Information for details) and estimated the marginal likelihood of each model using the path sampling method

(Lartillot & Philippe 2006). We used the marginal likelihoods to calculate the Bayes factor (BF) and used the 2lnBF test (Kass & Raftery 1995) to assess the relative support for a model of population expansion.

Approximate Bayesian computation and bottleneck analysis

We used an approximate Bayesian computation (ABC) approach (Beaumont *et al.* 2002) implemented in DIYABC v. 2.1.0 (Cornuet *et al.* 2014) to test for changes in population size associated with climatic and anthropogenically driven environmental change in NZ. We tested three general models (Cabrera & Palsbøll 2017): 'constant population size through time', 'population expansion' and 'population expansion and reduction' (Fig. 1).

We used 426 individuals for which mtDNA and/or microsatellite data were available (Supporting Information Tables S1 and S2). For each model, we generated 1 million datasets (see Supporting Information). We calculated Euclidean distances between the observed and normalized simulated summary statistics using the weighted local linear regression method (Beaumont *et al.* 2002), used the logistic approach to calculate point estimates and 95% confidence intervals (Cornuet *et al.* 2014), and retained 10 000 simulated datasets (1%) with the smallest Euclidean distance to calculate posterior parameter distributions. Confidence in the model choice was assessed by generating 500 pseudo-observed datasets and estimating type I and type II errors using the logistic regression approach (Cornuet *et al.* 2014).

The complete microsatellite dataset ($n = 422$) was used to test for a recent population bottleneck based on

the heterozygosity excess method implemented in BOTTLENECK v. 1.2.02 (Piry *et al.* 1999). We assumed a two-phase mutation model (TPM, Di Rienzo *et al.* 1994) with 95% single-step mutations (SMMs) and a variance of 12 (Piry *et al.* 1999), as well as used a wide range of parameter values as recommended by Peery *et al.* (2012) (Supporting Information). We assessed significance over all loci with a one-tailed Wilcoxon signed-rank test with 1000 replicates (Luikart & Cornuet 1998). We also determined the allele frequency distribution to identify signatures of recent bottlenecks using a mode-shift test (Luikart *et al.* 1998).

RESULTS

Past population size expansion

The neutrality statistics and MMA mostly provided evidence of population expansion. Although Tajima's D was negative but not statistically significant, there was strong support for a negative F_S ($P < 0.001$; Table 1). Mismatch distributions showed a good fit between the observed number of pairwise differences and expected frequencies of haplotypes under a rapid population expansion model (Fig. 2). The distribution was unimodal, and SSD and raggedness indices were non-significant for both markers, supporting historical rapid population expansion (Table 1). The haplotype network showed a star-like pattern, indicative of expansion (Fig. 2).

The EBSF showed a six-fold population size expansion in Black-fronted Terns starting about ~ 55 000 years ago (Fig. 3). Despite relatively large posterior density intervals, Bayes factor tests strongly

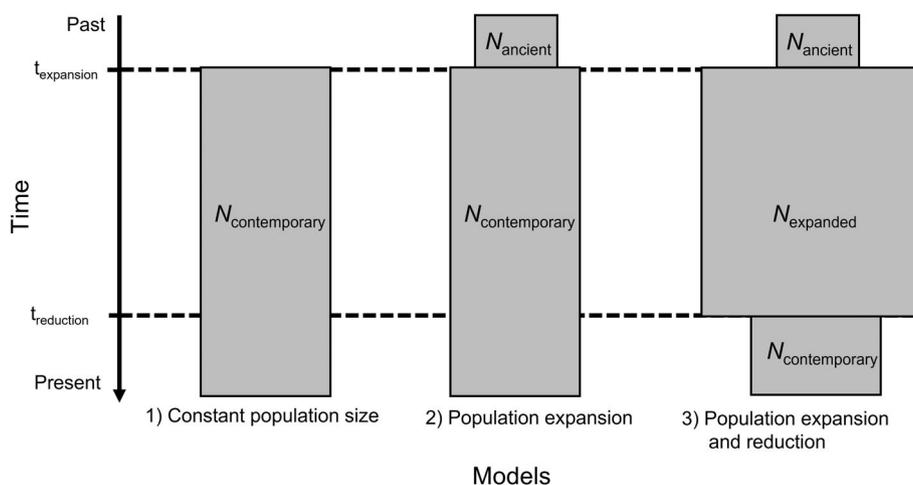


Figure 1. Three alternative scenarios of past population size changes as implemented in DIYABC. (1) Constant population size through time, (2) population expansion either during or after the glacial period and (3) population expansion and more recent contraction.

Table 1. Results of Black-fronted Tern past demographic analyses using neutrality statistics (Tajima's D and Fu's F_S estimates) and mismatch distributions (squared sum of deviances (SSD) and raggedness index (RI) estimates).

	Tajima's D	Fu's F_S	SSD	RI
Estimate	-1.091	-26.030	0.019	0.038
P -value	0.146	0.000	0.188	0.334

Associated P -values are shown, with those in bold indicating support for population expansion.

supported the model of population expansion (marginal likelihood estimate $EBSP = -3198.0022$ and Constant = -3212.3978 , $2\ln BF = 28.8$).

Recent decline

The 'population expansion and reduction' model (Fig. 1) was supported with a posterior probability of 91.92%, the model of 'population expansion' had a posterior probability of 5.60%, and the model of 'constant population size' received the least support with a posterior probability of 2.48%. The ancient effective population

size was estimated at 2020 individuals expanding to 335 000 individuals and then contracting to 9730 individuals (Table 2). The timing of expansion was estimated at $c.$ 3870 generations ago, which equates to 20 434, 36 107 or 38 700 years ago, assuming a generation time of 5.28, 9.33 and 10 years, respectively. The timing of the contraction was estimated at $c.$ 42 generations ago, which equates to 222, 392 and 420 years ago, assuming generation times of 5.28, 9.33 and 10 years, respectively (Table 2).

Type I and Type II error rates were 0.30 and 0.09, respectively. Model checking showed a good fit of the posterior distribution and observed data (Supporting Information Fig. S1). Bottleneck analyses did not support a recent strong bottleneck (one-tailed Wilcoxon signed-rank test $P = 0.940$, normal L-shaped distribution). Additional runs revealed support for a bottleneck only when assuming a proportion of SMM > 60% (Supporting Information Table S3), which is lower than the average estimate for vertebrates (Peery *et al.* 2012).

DISCUSSION

Multiple lines of evidence support a population expansion in Black-Fronted Terns, beginning during the last

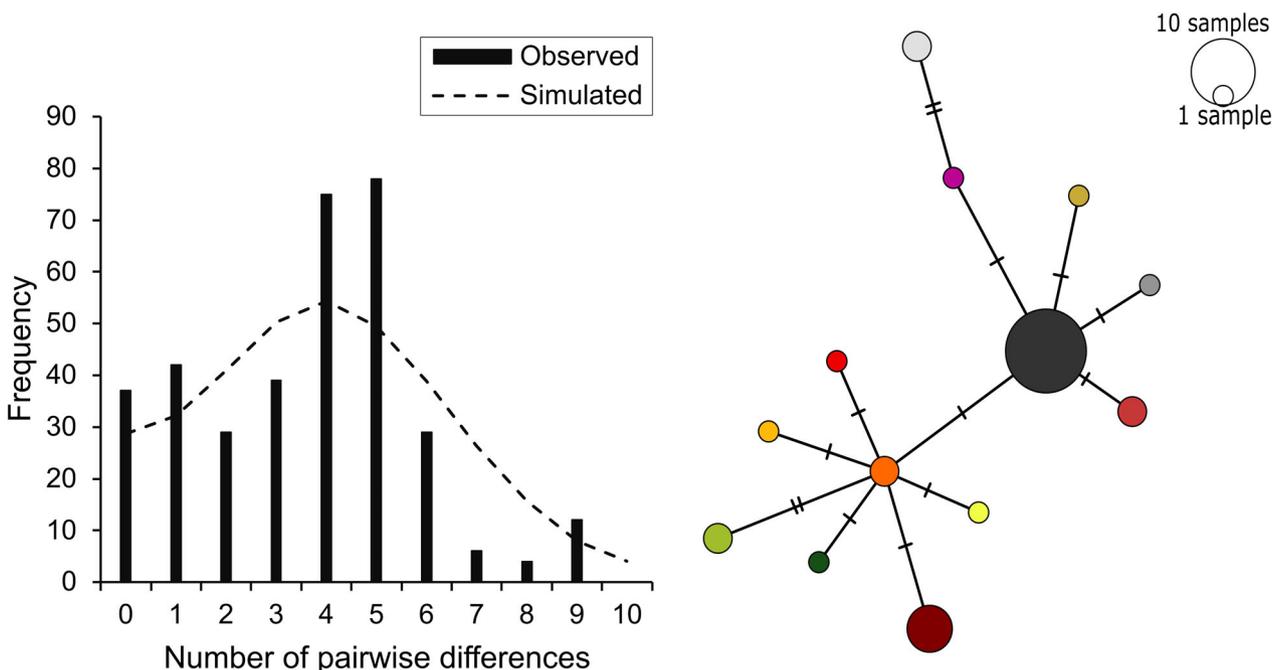


Figure 2. Mismatch distribution and median joining haplotype network of Black-fronted Terns mitochondrial DNA sequences (2041 bp Cytochrome b plus Control Region). Bars represent the observed frequencies of pairwise differences and the dashed line represents the expected frequencies under a model of sudden population expansion for the mismatch distribution. Colours of the haplotype network represent haplotype identity and size is proportional to the frequency as indicated by the legend. Edges represent single mutational steps.

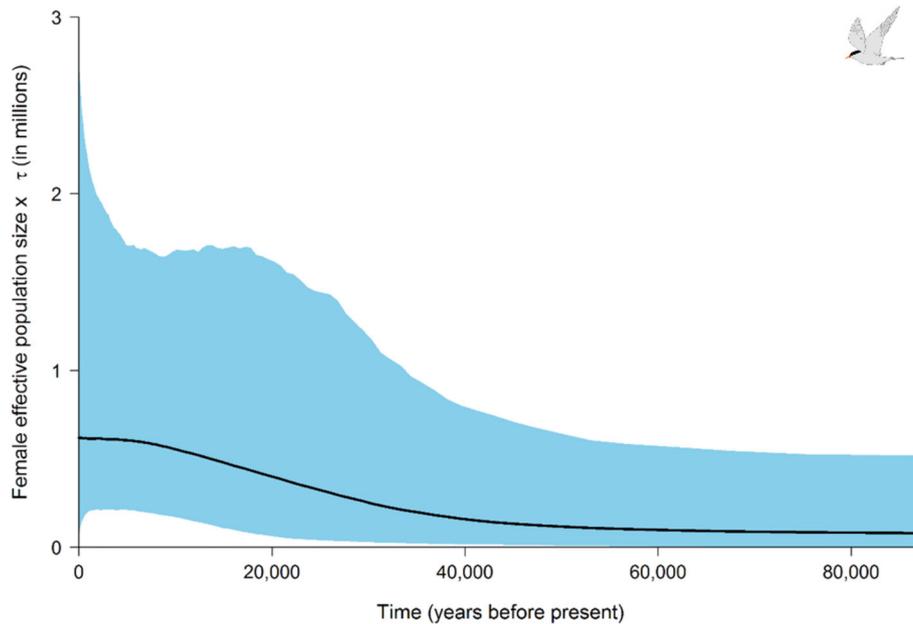


Figure 3. Demographic history of Black-fronted Terns over the last 85 000 years modelled from an extended Bayesian skyline plot based on Cytochrome b (1143 bp) and Control Region (898 bp) sequences from throughout their range. The female effective population size (N_{ef}) * generation length (τ) is shown on the y-axis and time in years before present on the x-axis. The solid line indicates the median estimate and the shaded area the 95% highest posterior density interval.

Table 2. Prior and posterior distributions of parameters for the demographic model ('population expansion and recent reduction'; Fig. 1) that gave the highest posterior probability when comparing different scenarios for Black-fronted Terns.

Parameter	Prior	Posterior mode	5% HPD	95% HPD
$N_{\text{contemporary}}$	Uniform (1000–10 000)	9730	1880	9880
N_{expanded}	Uniform (10000–500 000)	335 000	73 600	490 000
N_{ancient}	Uniform (1000–30 000)	2020	251	24 400
$t_{\text{reduction}}$	Uniform (1–4000)	42	7.3	263
$t_{\text{expansion}}$	Uniform (2000–20 000)	3870	2430	17 800

The timings of events are measured in generations. $N_{\text{contemporary}}$ = current population size, N_{expanded} = increased population size, N_{ancient} = initial population size, $t_{\text{reduction}}$ = timing of reduction as number of prior generations, $t_{\text{expansion}}$ = timing of expansion as number of prior generations, HPD = highest posterior density. Conditions: $t_{\text{expansion}} > t_{\text{reduction}}$; $N_{\text{ancient}} < N_{\text{expanded}}$.

glacial period (20 000–55 000 years BP). These data suggest that a model of range expansion during glacial periods ought to be considered for other open-habitat specialist birds in NZ, rather than the prevailing assumption of glacial refugia. A human-induced decline in population size is likely for Black-fronted Terns.

Responses to the formation of new areas of favourable habitat under different climatic conditions have been observed in other avian species adapted to open environments (Kearns *et al.* 2014). For shorebirds, population expansions are thought to have occurred in Arctic breeding species in the Northern Hemisphere associated with more extended tundra habitat during glacial

periods (Kraaijeveld & Nieboer 2000, Rönkä *et al.* 2012). In the Southern Hemisphere, population expansions have been linked to extended habitat in temperate regions during glacial periods and in tropical regions during post-glacial periods as coral reefs formed (Peck & Congdon 2004). For Black-fronted Terns, all analyses supported a population expansion during glaciation, independent of the assumed generation length. Both the EBSP and DIYABC analyses provided estimates that coincided with expansion of coastline and the braided river plains beyond their present-day limits and dry grasslands dominating the lowland landscape (Browne & Naish 2003, Wood *et al.* 2017). Black-

fronted Terns are adapted to open, non-forest habitat for breeding and feeding. While breeding colonies are established on bare gravel bars near rivers, terns use both freshwater and grass- or shrubland areas for foraging (Lalas 1977, O'Donnell & Hoare 2009). Terns are also able to rapidly use newly cleared, open areas for nesting (Schlesselmann *et al.* 2018). It is therefore not surprising that the estimates of population expansion for Black-fronted Terns date much earlier than inferred for other NZ forest or alpine species (~ 35 000 vs. ~ 14 000 years ago), which are assumed to have contracted into refugia during glacial periods (e.g. Goldberg *et al.* 2011, Dussex *et al.* 2014, Weston & Robertson 2015).

We obtained the strongest support for the 'population expansion and reduction' model in our ABC analysis. All of our estimates of the timing of reduction based on the range of plausible generation lengths suggest a reduction in population size after colonization of NZ by humans and their commensal species (Greig & Rawlence 2021). Black-fronted Terns bred on the volcanic plateau of the central North Island until about 1930 (Stead 1932) but since then have only bred on the South Island. A decrease in population size with a simultaneous contraction in range seems plausible. In contrast, our BOTTLENECK analyses did not consistently support a recent bottleneck. However, several studies have reported that such tests do not always detect bottlenecks in vertebrate populations known to have experienced declines (e.g. Taylor *et al.* 2007). Mátics *et al.* (2017) suggested that the detection of a bottleneck is independent of the proportional decline but rather depends on the absolute size of the surviving population. In the case of Black-fronted Terns, the surviving population appears to be still relatively large (Schlesselmann & Robertson 2020) when considering population bottlenecks of island populations of only dozens of individuals. The population is nevertheless in range-wide decline (O'Donnell & Hoare 2011). As with other historical demography analyses based on genetic data, our analyses are limited by the accuracy of estimated mutation rate of loci and the number of loci used (Grant 2015). Using whole genomes in future analyses may increase inferential power (Ghirotto *et al.* 2020).

To the best of our knowledge, this is the first study of an open habitat specialist bird in NZ to test for habitat-induced population expansion during Pleistocene glaciation. It seems plausible that other NZ open habitat specialists were probably not restricted to refugia (e.g. other Charadriiformes). Future work should focus on developing theoretical foundations for past and present range expansions of open habitat specialists taking species' ecologies and changing ecological communities into account (Kearns *et al.* 2014, Rawlence *et al.* 2019). Testing theoretical predictions may reveal congruent

responses among co-distributed species and provide further insights into environmental and anthropogenic drivers of demographic history.

We gratefully acknowledge Ngāi Tahu who permitted genetic analyses of Tarapirohe blood samples obtained from their lands. We thank G. Voelker, W. Lee, R. C. K. Bowie and an anonymous reviewer for comments on an earlier version of the manuscript. Thanks also to D. Barrell and J. Wilmshurst on information of New Zealand during the Quaternary. Open access publishing facilitated by Landcare Research New Zealand, as part of the Wiley - Landcare Research New Zealand agreement via the Council of Australian University Librarians.

AUTHOR CONTRIBUTIONS

Ann-Kathrin V. Schlesselmann: Conceptualization (equal); data curation (equal); formal analysis (lead); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Jamie Cooper:** Data curation (equal); investigation (equal); methodology (equal); project administration (equal); writing – review and editing (equal). **Nicolas Dussex:** Formal analysis (supporting); investigation (supporting); methodology (supporting); writing – review and editing (supporting). **Bruce C. Robertson:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); funding acquisition (equal); investigation (supporting); methodology (supporting); project administration (supporting); resources (supporting); supervision (lead); writing – review and editing (supporting).

CONFLICT OF INTEREST

None.

ETHICAL NOTE

All animal capturing, handling and sampling techniques were undertaken according to the ethical guidelines of the University of Otago (Ethics approval number 61/14). Sampling of birds, and storage and use of blood samples were done with permission of the New Zealand Department of Conservation (Wildlife Act permit nr: OT-25557-DOA and 78375-DOA).

FUNDING

The research was funded by a grant (New Zealand Department of Conservation Contract No. 11138) to B.C.R. A.K.V.S. was supported by a University of Otago PhD Scholarship.

Data Availability Statement

The mitochondrial data are available on GenBank under accession numbers MN452902–MN453001. The microsatellite data are available as Supporting Information Appendix S1.

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Received 6 October 2021;
revision accepted 3 July 2022.
Associate Editor: Gary Voelker.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Microsatellite genotypes.

Figure S1. Principal components analysis for pre-evaluation of all scenarios using only the subset of summary statistics chosen.

Figure S2. Principal components analysis for model checking on scenario 3 using all summary statistics.

Table S1. Overview of 73 samples and genetic data available for each sample. Each sample is labelled as BFT for Black-fronted Tern and sample number.

Table S2. Additional microsatellite samples used in BOTTLENECK analysis.

Table S3. Results of BOTTLENECK runs using a two-phased mutation model with a range of values for the proportion of single-step mutations (SMM); *P*-values of one-tailed Wilcoxon sign-rank tests with significance indicated in bold.