



RESEARCH ARTICLE

Predicting harvest impact and establishment success when translocating highly mobile and endangered species

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Handling Editor: Matt Hayward**Abstract**

1. Harvesting individuals for translocations can negatively impact source populations, a critical challenge for species reduced to small populations. Consequently, translocation cohorts often remain small, reducing the establishment probability at the destination. Balancing the potential benefits and risks of such translocations is further complicated by philopatry and natural metapopulation dynamics if the target species is highly mobile. These challenges highlight the importance of translocation feasibility assessments, but such assessments often remain qualitative to date.
2. The critically endangered Kuaka (Whenua Hou Diving Petrel; *Pelecanoides whenuahouensis*) is a philopatric, highly mobile seabird that could benefit from conservation translocations, but only one small population remains. Through expert elicitations with a user-friendly Shiny app, we developed a novel metapopulation extension to an integrated population model fitted to long-term data, allowing us to simultaneously project harvest impact on the source and establishment of destination populations under alternative translocation scenarios, while accounting for philopatry and metapopulation dynamics.
3. Establishment of a destination population without excessive impact on the source was possible, but subject to uncertainty about philopatry and metapopulation dynamics. Accounting for juveniles returning to the source post-translocations reduced impact on the source, but also decreased establishment at the destination. Natural movements of adults and juveniles between source and destination populations were predicted to modulate effects of different harvest intensities.

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4. *Synthesis and application.* Using state-of-the art integrated population models and expert elicitations, we illustrate how translocation feasibility can be evaluated transparently and quantitatively, even when targeting endangered, philopatric and highly mobile species. Our approach is a considerable improvement on current qualitative feasibility assessments. However, we also illustrate that, ultimately, the favoured translocation strategy depends on balancing biological and other fundamental objectives inherent to translocations. Therefore, the ideal strategy cannot be determined solely mathematically, and feasibility assessments should incorporate explicit value statements. Our methodology is applicable to any future translocation scenario.

KEYWORDS

Bayesian inference, conservation, integrated population model, metapopulation dynamics, *Pelecanoides whenuahouensis*, philopatry, reintroduction, seabirds

1 | INTRODUCTION

Conservation translocations are a powerful strategy to counteract the accelerating and pervasive biodiversity loss in the Anthropocene (Armstrong & Seddon, 2008; Seddon et al., 2014). A conservation translocation is defined as the intentional movement and release of a living organism for conservation and/or restoration objectives (IUCN, 2013; Seddon et al., 2014). Conservation translocations are considered feasible if it is predicted that: (a) a suitable destination site is available, (b) the candidate species is unlikely to naturally colonise this site on an acceptable timescale, (c) the translocation will not endanger the source population and (d) the species is likely to establish a population at the destination site (IUCN, 2013). However, such predictions may be highly uncertain, hence translocation decisions involve balancing risks.

For species that only survive in small remnant populations, it is necessary to balance the trade-off between minimising impact on source populations and harvesting sufficient individuals to establish populations at destination sites. Harvesting source populations can lower genetic diversity, increase demographic stochasticity and reduce vital rates (e.g. Dimond & Armstrong, 2007; Furlan et al., 2020), but translocating too few individuals will reduce the probability of establishing a population at the destination site (e.g. Yackulic et al., 2021). This trade-off can sometimes be solved by establishing captive populations that become sources for translocations, but captivity is not an option for every species (Canessa, Converse, et al., 2016). Identifying the appropriate number of individuals to translocate to a wild site is complicated because the optimal numbers depend on the vital rates expected at the destination sites and those rates are highly uncertain for translocations involving endangered species (Parlato & Armstrong, 2018). It is therefore essential for translocation planning to be able to forecast both the demographic impacts on source populations and the establishment of destination populations in face of uncertainty (IUCN, 2013;

Panfylova et al., 2019). Yet, despite their importance to feasibility assessments, such dual forecasting exercises are rarely conducted (Lamonthe et al., 2021), and if they are conducted, these assessments are usually qualitative (IUCN, 2013).

Assessments of translocation feasibility are further challenged if target species exhibit strong philopatry or high mobility. Philopatry can result in individuals returning to the source post-translocation, either immediately or once mature, potentially causing translocation failure (Oro et al., 2011; Ruffel & Parsons, 2009). High mobility may create further challenges for predicting translocation outcomes. Specifically, even when natural colonisation of a destination site is unlikely, once individuals are translocated, social attraction could result in new metapopulation dynamics (Miskelly et al., 2009; Oro, 2020; Oro et al., 2011). Unanticipated movements between populations could influence impact on the source and establishment at the destination, exacerbating uncertainty of translocation outcomes.

Conservation translocations of seabirds are increasingly popular, but are complicated by the species' innate philopatry, high mobility and unsuitability for captive breeding programs (Miskelly et al., 2009). Seabird translocations are motivated by the desire to restore seabirds' roles as ecosystem engineers and the high threat status of many seabird species (Jacobs et al., 2020; Jones & Kress, 2012). Consequently, the number of seabird translocations has been steadily increasing with >200 attempts to date (Seabird Restoration Database, 2022; Zhou et al., 2017). As with many conservation translocations, data to evaluate past and inform future seabird translocations are limited due to patchy monitoring (Paleczny et al., 2015). Even where monitoring data are available, our limited understanding of philopatry and metapopulation dynamics following translocations of seabirds complicate translocation feasibility assessments (Oro et al., 2011).

The Kuaka (Whenua Hou Diving Petrel; *Pelecanoides whenuahouensis*) is a critically endangered, philopatric and highly mobile

seabird restricted to a single breeding colony. Despite the apparent availability of suitable breeding habitat, Kuaka appear unlikely to colonise new sites on their own or by using acoustic attraction (Fischer, Taylor, Debski, & Wittmer, 2020). Conservation translocations could help establish new colonies, but vital rates are only available for the source population. Furthermore, the sole remaining Kuaka population is extremely small (~200 adults; Fischer, Taylor, Cole, et al., 2020) and harvesting individuals for translocations may cause the source population to decline.

We used long-term data and expert elicitations within a meta-population extension of an integrated population model (IPM) to estimate vital rates of source and destination, predict harvest impact on the source and project establishment of a destination population, under various translocation scenarios, while accounting for philopatry and metapopulation dynamics (Figure 1). Our feasibility assessment illustrates how risky translocations can be transparently and quantitatively evaluated, even when the target species is endangered, philopatric and highly mobile.

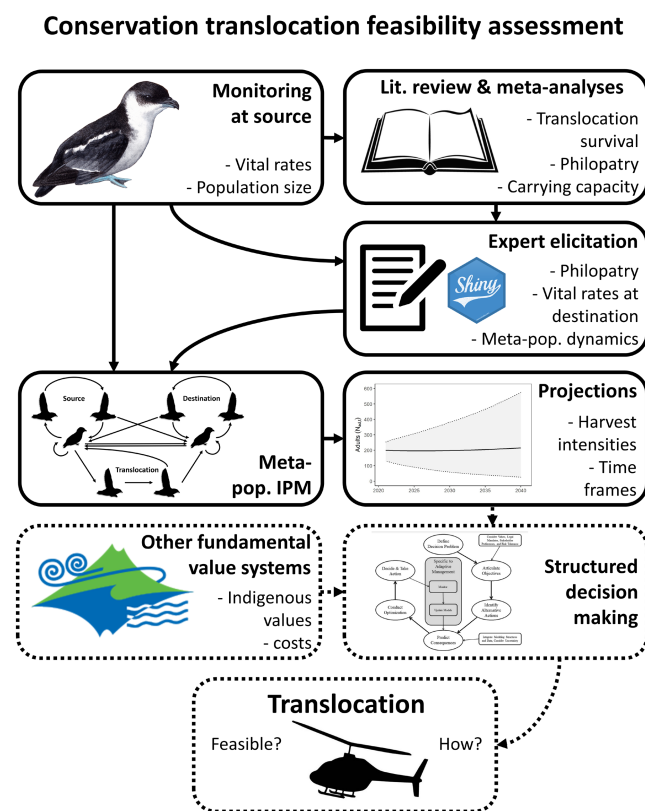


FIGURE 1 Flow diagram of our translocation feasibility assessment, combining monitoring, meta-analyses, expert elicitations through a shiny app (https://docnewzealand.shinyapps.io/Kuaka_Population_App/) and integrated population models (IPM) to generate projections for source and destination populations. These projections can be used in future (dotted boxes) structured decision-making (SDM) frameworks to balance biological values with other fundamentally important values to ultimately identify the ideal translocation strategy. SDM diagram adapted from Converse et al. (2013). Kuaka artwork: A. Jearwattakanok.

2 | MATERIALS AND METHODS

2.1 | Study species

The critically endangered Kuaka once acted as an ecosystem engineer throughout dunes in southern Aotearoa (New Zealand). Invasive predators have now restricted Kuaka to a single colony on Whenua Hou (Codfish Island; -46.766°S , 167.645°E). Invasive predators were eradicated from Whenua Hou in 2000. Despite these efforts, the Kuaka population is extremely small (194–208 adults), and population growth remains negligible, indicating ongoing threats, as the population is not near carrying capacity (Fischer, Taylor, Cole, et al., 2020). Kuaka only breed in foredunes <20m from the springtide line, rendering birds vulnerable to storm-induced erosion and climate change (Fischer, Debski, Taylor, et al., 2018). Competition for burrows with other seabirds and vessel-based light pollution may pose additional threats (Fischer, Debski, et al., 2021; Fischer, Wittmer, et al., 2021). Kuaka did not respond to an acoustic attraction system aimed to lure them to more secure breeding sites on Whenua Hou (Fischer, Taylor, Debski, & Wittmer, 2020). Therefore, translocating pre-fledgling chicks to another island free of invasive predators is being considered as a potential strategy to conserve Kuaka.

An understanding of life history is critical to finetuning predictive models required for assessments of translocation feasibility (IUCN, 2013; Miskelly et al., 2009). Kuaka are relatively long-lived animals (>20 years). They breed from September to January, laying a single egg per pair (Fischer, Wittmer, et al., 2021). Kuaka are highly mobile and after the breeding period adults migrate thousands of kilometres to the Polar Front (Fischer, Debski, et al., 2021). Juveniles likely spend the first years of their lives entirely at sea at an unknown location. Kuaka mirror other Diving Petrels and generally start breeding at age 2 (Miskelly et al., 2009). All adult Kuaka appear to attend burrows at the breeding colony every year and, unlike some other Procellariiformes (e.g. Warham, 1996), do not take sabbaticals. Kuaka exhibit an unusually fast life cycle for a Procellariiform seabird, but vital rates and metapopulation dynamics remain poorly understood, limiting predictions on translocation outcomes.

2.2 | Capture–recapture data

To quantify detection, adult survival, juvenile survival, sex ratios and population size, we used intermittent capture–recapture data of 396 adults and 112 fledglings. Specifically, we captured and banded adults on Whenua Hou during September–January 2002–2004, 2008 and 2015–2020 (referring to years in which breeding started; see Appendix S1). We defined adults as birds returning to the colony, as age cannot be determined phenotypically (Fischer, Debski, Miskelly, et al., 2018). To reduce capture biases, we used a variety of capture techniques: hand capture, sometimes aided by playback/mimics, burrow traps and spotlighting (i.e. attracting birds to handheld spotlights). In 2015–2020, we also captured and banded fledglings at their burrows. We considered each breeding period as

a separate sampling occasion to estimate annual survival probabilities. As Kuaka are sexually monomorphic (Fischer, Debski, Miskelly, et al., 2018), we collected contour feathers from 246 adults and 99 fledglings and used these for genetic sex determination (following Norris-Caneda & Elliott, 1998). We successfully sexed 116 female and 130 male adults and 50 female and 49 male fledglings.

2.3 | Productivity data

To quantify breeding probability (i.e. the probability of an adult female laying an egg) and breeding success (i.e. the probability of an egg producing a fledgling), we monitored a total of 204 Kuaka burrows 2017–2019 (65%–79% of annual nest attempts). We checked burrows weekly throughout the breeding period using a burrowscope (Sextant Technologies, Wellington, New Zealand; Fischer, Wittmer, et al., 2021). The productivity data we collected were per burrow, rather than per individual. We therefore had to assume that the probability of an egg being laid in a burrow was equal to an adult female laying an egg. As endangered species often exhibit skewed

the Bayesian modelling software OpenBUGS 3.2.3 (Spiegelhalter et al., 2014). IPMs can incorporate incomplete data from a range of sources into a single dynamic model while enabling full expression of uncertainty and incorporation of parameter covariance (Armstrong et al., 2021; Parlato et al., 2021; Saunders et al., 2018; Schaub & Abadi, 2011). Our IPM consisted of three model components: (a) an open-population Cormack–Jolly–Seber model using the capture–recapture data, (b) two generalised linear mixed-effects models (GLMMs) using the productivity data and (c) an abundance model using counts of banded and unbanded Kuaka. We incorporated environmental and demographic stochasticity in our IPM using random-effect processes and binomial stochastic nodes respectively. Using a metapopulation approach, we included a destination population in our IPM and linked source and destination populations with estimates of (a) juveniles arising from translocated fledglings, (b) juveniles returning to the source under the effects of philopatry and (c) metapopulation dynamics of adults and juveniles moving between populations. Central to our IPM was a pre-breeding census, age-structured 7×7 Leslie matrix that integrated both source and destination populations (Caswell, 2001):

$$\begin{bmatrix} N_{juv0,S} \\ N_{juv1,S} \\ N_{ad,S} \\ N_{juv0,T} \\ N_{juv1,T} \\ N_{juv0,D} \\ N_{juv1,D} \\ N_{ad,D} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & P_{fem}f_S\gamma_S(1-\psi_h) & 0 & 0 & 0 & 0 & 0 \\ \Phi_{juv} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \Phi_{juv}(1-\psi_{juv,S}) & \Phi_{ad,S}(1-\psi_{ad,S}) & 0 & \Phi_{juv}\psi_r & 0 & \Phi_{juv}\psi_{juv,D} & \Phi_{ad,D}\psi_{ad,D} \\ 0 & 0 & P_{fem}f_S\gamma_S\psi_h\Phi_T & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_{juv} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & P_{fem}f_D\gamma_D \\ 0 & 0 & 0 & 0 & 0 & \Phi_{juv} & 0 & 0 \\ 0 & \Phi_{juv}\psi_{juv,S} & \Phi_{ad,S}\psi_{ad,S} & 0 & \Phi_{juv}(1-\psi_r) & 0 & \Phi_{juv}(1-\psi_{juv,D}) & \Phi_{ad,D}(1-\psi_{ad,D}) \end{bmatrix} \times \begin{bmatrix} N_{juv0,S} \\ N_{juv1,S} \\ N_{ad,S} \\ N_{juv0,T} \\ N_{juv1,T} \\ N_{juv0,D} \\ N_{juv1,D} \\ N_{ad,D} \end{bmatrix} \quad (1)$$

sex ratios (Lawrence et al., 2008) or same sex pairings (Young et al., 2008), which could violate our assumption, we tested our assumption by using estimates of population size, number of burrows (following Fischer, Taylor, Cole, et al., 2020) and sex ratio to estimate the number of adult females per burrow: 1.02 (0.91–1.13). This estimate supported our assumption.

2.4 | Ethics statement

All methods were approved by the Whenua Hou Komiti, Kaitiaki Rōpū, an animal ethics committee (VUW-AEC-22252, VUW-AEC-23283, and VUW-AEC-27621), and the New Zealand Department of Conservation (45407-FAU, 45907-FAU, 47920-LND-1516/04, 52,029-LND, M1718/01, M1819/01, M1920/02 and M2021/01).

2.5 | Integrated population model

To estimate Kuaka vital rates and population size and assess translocation feasibility, we fitted an age-structured IPM using

A visualisation of this matrix and a key to all acronyms is provided in Figure 2.

2.5.1 | Estimation of survival at the source

We applied an open-population Cormack–Jolly–Seber model (Lebreton et al., 1992) in the state-space formulation (Gimenez et al., 2007; Kery & Schaub, 2012) to the capture–recapture data to estimate annual detection p_t , adult survival $\varphi_{ad,t}$ and juvenile survival probabilities $\varphi_{juv,t}$:

$$Y_{i,t} \mid X_{i,t} \sim \text{Bernoulli}(X_{i,t}p_t), \quad (2)$$

$$X_{i,t+1} \mid X_{i,t} \sim \text{Bernoulli}(X_{i,t}\varphi_{i,t}). \quad (3)$$

Equation 2 described the observation process and Equation 3 described the state process. $Y_{i,t}$ equalled 0 if individual i was not detected at time t , and 1 if it was. $X_{i,t}$ equalled 0 if the individual was dead at time t , and 1 if the individual was alive. p_t is the detection probability at time t . $\varphi_{i,t}$ is the survival probability of individual i over the time interval t to $t+1$. We estimated p_t using:

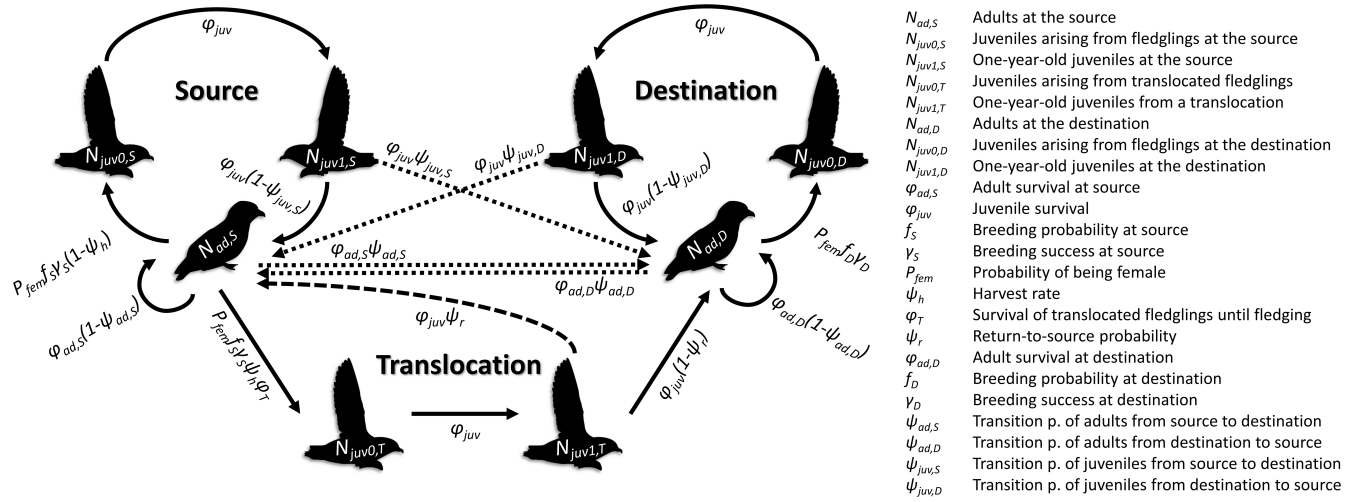


FIGURE 2 Conceptual framework of the metapopulation IPM used to estimate harvest impact and establishment success of Kuaka translocations. Silhouettes indicate age classes while arrows indicate vital rates and transition probabilities and the various scenarios that were explored: No metapopulation dynamics (solid), accounting for return-to-source probability (dashed), full metapopulation dynamics (dotted).

$$\text{logit}(p_t) = \alpha_p + \epsilon_{p,t} \tag{4}$$

in which, α_p is the intercept of the detection equation and $\epsilon_{p,t}$ is an annual random effect on detection. We used vague priors for α_p ($N[\text{mean} = 0, \text{precision} = 0.1]$) and $\sigma_{\epsilon_{p,t}}$ ($U[0, 3]$). We fixed p_t at 0 for years without surveys (2005–2007 and 2009–2014) and for 1-year-old juveniles, which we assumed to be out at sea (i.e. we fixed age at first return at 2 years of age). We did not include age effects on p_t due to the low sample size of recaptured known-age birds ($n = 20$). We estimated $\varphi_{i,t}$ using:

$$\text{logit}(\varphi_{i,t}) = \alpha_\varphi + \beta_{juv} juv_{i,t} + \epsilon_{\varphi,t} \tag{5}$$

in which α_φ is the intercept of the survival equation, β_{juv} is the age effect on survival, $juv_{i,t}$ is the juvenile status of individual i at time t , and $\epsilon_{\varphi,t}$ is an annual random effect on survival. We used vague priors for α_φ ($N[0, 0.1]$), β_{juv} ($N[0, 1]$) and $\sigma_{\epsilon_{\varphi,t}}$ ($U[0, 3]$). We thus assumed that survival during the first 2 years of life was different from older birds and estimated annual adult survival $\varphi_{ad,t}$ and juvenile survival $\varphi_{juv,t}$ as:

$$\text{logit}(\varphi_{ad,t}) = \alpha_\varphi + \epsilon_{\varphi,t}, \tag{6}$$

$$\text{logit}(\varphi_{juv,t}) = \alpha_\varphi + \beta_{juv} + \epsilon_{\varphi,t}. \tag{7}$$

2.5.2 | Estimation of productivity at the source

We first estimated the probability of an individual being female (P_{fem}) using a Bernoulli process and the genetic sex determination data. We then fitted two GLMMs with Bernoulli error terms to the productivity data to estimate annual breeding probability (f_i ; probability of an adult female laying an egg) and breeding success (γ_i ; probability of an egg producing a fledgling):

$$\text{logit}(f_t) = \alpha_f + \epsilon_{f_t} \tag{8}$$

$$\text{logit}(\gamma_t) = \alpha_\gamma + \epsilon_{\gamma_t} \tag{9}$$

in which α_f and α_γ are the intercepts and ϵ_{f_t} and ϵ_{γ_t} are the annual random effects. We used vague priors for α_f and α_γ ($N[0, 0.1]$), but as we only had 3 years of nest monitoring data (2017–2019), we used a mildly informative prior for $\sigma_{\epsilon_{f_t}}$ and $\sigma_{\epsilon_{\gamma_t}}$ ($U[0, 0.2]$).

2.5.3 | Estimation of source population size and growth

Following best practice modelling frameworks for modern IPMs (Parlato et al., 2021), we used the annual counts of unbanded (i.e. adults captured for the first time) and banded adults in conjunction with detection, survival and productivity estimates to infer adult population size at the source ($N_{ad,S,t}$). Specifically, we first estimated the number of 2-year-old juveniles recruiting into the source. We used this estimate with the estimated number of surviving undetected adults to infer an annual pool of unbanded adults available for detection. We sampled the annual number of captured unbanded adults from this pool using the detection probability. Ultimately, we combined the estimated pool of undetected unbanded adults and the sum of surviving banded adults to infer $N_{ad,S,t}$. To start this process, we used an informative prior for the number of 2-year-old juveniles recruiting into the source ($U[0, 60]$) and the unknown undetected adults ($U[0, 200]$) for the first year in our study (2002). This approach allowed us to use all available information to estimate population size for years with data and infer population size for years without. Finally, we stochastically estimated the average finite rate of population growth λ at the source site following Parlato and Armstrong (2018):

$$\lambda = \frac{\varphi_{ad} + \sqrt{\varphi_{ad}^2 + 4P_{fem}f\gamma\varphi_{juv}^2}}{2}. \quad (10)$$

2.6 | Meta-analyses and expert elicitations

To meaningfully explore translocation impact and establishment success, we had to estimate additional parameters beyond vital rates and population size at the source (Figure 1). We used a combination of meta-analyses and online expert elicitations (Hemming et al., 2018) to estimate additional parameters: fledgling translocation survival (from harvest at the source to fledging at the destination), the return-to-source probability (i.e. the probability of juveniles returning to the source post-translocation due to philopatry), the probability of adults and juveniles recruiting from the source to the destination and vice versa, breeding probability, breeding success and adult survival at the destination, and carrying capacity at the source and destination. We assumed that juvenile survival was equal between source and destination populations due to the pelagic nature of this life cycle stage (Warham, 1996), but as adults spend considerable time on land at breeding colonies, we allowed adult survival to differ between source and destination. We used three steps to gain the best possible estimates for the required parameters:

First, we compiled and summarised available data on Kuaka alongside data published on other (Diving) Petrels (Appendix S1). For fledgling translocation survival, we conducted a meta-analysis using published data on Petrel translocations. For estimates of the return-to-source probability, we generated a mean estimate for Petrel translocations following another meta-analysis. For estimates of metapopulation dynamics and vital rates at the destination, we collated habitat and seabird distribution data for a potential candidate site alongside preliminary IPM-derived estimates of vital rates at the source. This candidate site (Rarotoka; Centre Island; 46.454°S, 167.848°E; 38 km north of Whenua Hou) is located within the historic range of the species, free of invasive predators, and within the species' current foraging distribution during the breeding period. For estimates of carrying capacity, we first aimed to elicit estimates of maximum burrow densities, for which we compiled current Kuaka burrow density (0.003; 0.001–0.011 burrows per m²) alongside estimates of other Diving Petrel populations. We used these data to help guide expert elicitations, but to lessen the burden on experts, we used the estimate for Common Diving Petrel (*P. urinatrix*) fledgling translocation survival directly from our meta-analysis (Miskelly et al., 2009; Appendix S1).

Second, we built a user-friendly Shiny app (https://docnewzealand.shinyapps.io/Kuaka_Population_App/) to communicate compiled information and host an online expert elicitation following a modified Delphi protocol (Hemming et al., 2018). In the app, we first provided a training exercise and then asked Diving Petrel experts ($n = 8$) to provide us with estimates of the required parameters within the app (round one). Specifically, our Shiny app contained clear visualisations of density distributions and proportional plots of the compiled information and allowed experts to provide us explicitly and intuitively with a four-point estimate per parameter

(minimum plausible value, best guess, maximum plausible value and confidence that the range contained the true value; Speirs-Bridge et al., 2011). Once all experts had provided us with their responses, we aggregated their answers anonymously, and organised an online discussion. After this discussion, experts could revisit and adjust their original answers within the Shiny app to provide us with their final estimate (round two).

Third, we used a series of novel transformations to incorporate the expert-elicited parameters directly within our IPM. We rescaled each individual expert response to 100% confidence (Speirs-Bridge et al., 2011) and created beta-PERT distributions for each response using the minimum, best guess and maximum (Clark, 1962). We aggregated answers from experts into a single distribution by sampling 10,000 values from individual distributions for each expert and refitting them as gamma- or beta-distributions, depending on the parameter. To convert estimates of maximum burrow density into carrying capacity (K), we multiplied density estimates by the suitable area at source and destination sites (26,828 and 12,243 m² respectively; JH Fischer unpublished data) and the estimated number of adults per burrow (2.03; 1.96–2.11; following Fischer, Taylor, Cole, et al., 2020). We transformed elicited demographic rates for the destination into coefficients for the GLMMs in our IPM by assuming perfect covariance of expert-elicited and IPM-derived estimates. This allowed us to use the differences between cumulative density functions (CDFs) of pairs of estimates (e.g. $\varphi_{ad,S}$ and $\varphi_{ad,D}$) to derive normal-distributed coefficients $\beta_{\varphi_{ad,D}}$, β_{f_D} and β_{γ_D} for adult survival, breeding probability and breeding success respectively. We incorporated these coefficients directly within our IPM for projections of the destination population, allowing for propagation of interannual variation using the random effects estimated for the source:

$$\text{logit}(\varphi_{ad,D,t}) = \alpha_{\varphi} + \beta_{\varphi_{ad,D}} + \varepsilon_{\varphi,t}, \quad (11)$$

$$\text{logit}(f_{D,t}) = \alpha_f + \beta_{f_D} + \varepsilon_{f,t}, \quad (12)$$

$$\text{logit}(\gamma_{D,t}) = \alpha_{\gamma} + \beta_{\gamma_D} + \varepsilon_{\gamma,t}, \quad (13)$$

Our approach thus allowed us to estimate parameters that are currently impossible to empirically estimate and integrate all sources of data directly within one metapopulation IPM.

2.7 | Projections

By linking source and destination populations through harvested fledglings and metapopulation dynamics, we could fit our IPM to the data for the duration of the study at the source (2002–2020) and simultaneously project both populations for 30 years (2021–2050). We introduced a ceiling for projections of both populations based on the site-specific K , that is, we assumed no density dependence operated until K was reached. We then projected source and destination populations under different scenarios and population dynamics

assumptions. Specifically, we project populations while varying harvest intensities (0%–30% of all fledglings) and timeframes (5–10 consecutive years of harvesting) and either (a) excluding metapopulation dynamics, or (b) accounting for the return-to-source probability, or (c) including full metapopulation dynamics. For each scenario-assumption combination, we calculated the extinction probability after 30 years (proportion of MCMC values of $N_{ad,t} = 0$) for source, destination and the total populations. Finally, we used the probability distributions of population sizes of source, destination and total populations in 2050 under different scenarios-assumption combinations to create CDFs and assess stochastic dominance (Canessa, Ewen, et al., 2016). Our investigation allowed for a unified approach to assess translocation feasibility for a critically endangered, philopatric and highly mobile species.

We fitted our IPM in OpenBUGS by running two MCMC chains for 75,000 iterations after a burn-in of 50,000 iterations, which was sufficient to reach convergence (based on $\hat{R} < 1.05$ and visual inspections of trace plots). We report the means of posterior distributions with 95% credible intervals.

3 | RESULTS

3.1 | Vital rates and population size at the source

At the source (Whenua Hou), adult survival was estimated at $\hat{\phi}_{ad,S} = 0.865$ (0.830–0.907), juvenile survival was estimated at $\hat{\phi}_{juv,S} = 0.747$ (0.672–0.826), breeding probability (probability of an adult female laying an egg) was estimated at $\hat{f}_S = 0.832$ (0.778–0.880) and breeding success (probability of an egg producing a fledgling) was estimated at $\hat{\gamma}_S = 0.657$ (0.589–0.728; Figure 3). The proportion of females was estimated at $\hat{P}_{fem} = 0.500$ (0.450–0.551). The source population size ($\hat{N}_{ad,S,t}$) was estimated at 176 (113–234) adults in 2002 and 198 (156–228) adults in 2020. This increase was reflected in the estimated annual population growth $\hat{\lambda} = 1.017$ (0.971–1.085). Based on our expert elicitation, maximum burrow density at the source was highly uncertain, with an estimated 0.195 (0.005–0.947) burrows per m^2 , leading to a carrying capacity \hat{K}_S of 10,600 (272–51,700) adults. When projecting the source population under *status quo*, population size was predicted at 236 (11–896)

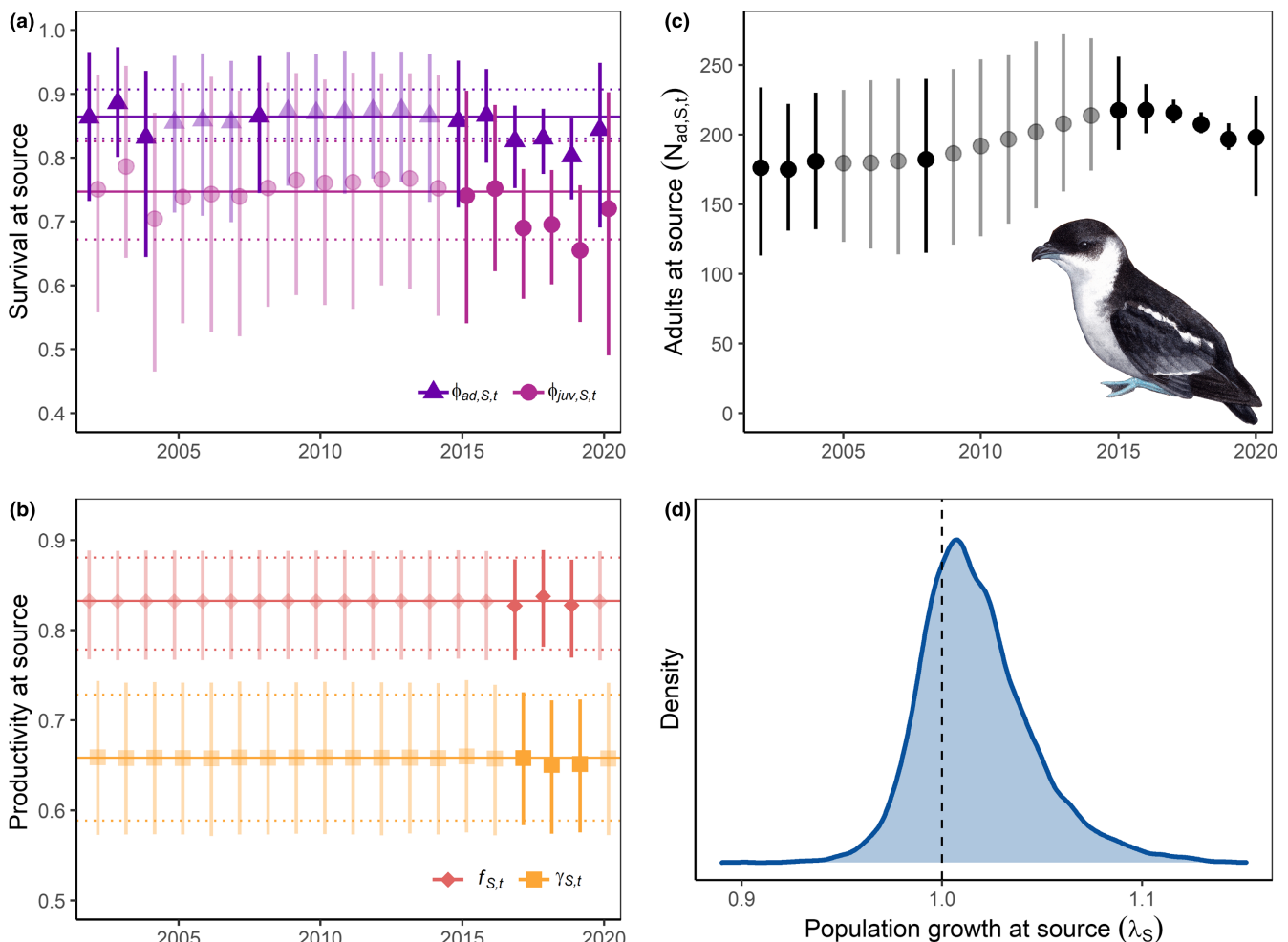


FIGURE 3 Estimates of adult survival ($\hat{\phi}_{ad,S,t}$; a), juvenile survival ($\hat{\phi}_{juv,S,t}$; a), breeding probability ($\hat{f}_{S,t}$; b), breeding success ($\hat{\gamma}_{S,t}$; b), adult population size ($\hat{N}_{ad,S,t}$; c) and population growth ($\hat{\lambda}_S$; d) at the source population. Horizontal solid and dotted lines indicate multi-year means. Solid symbols indicate estimates for years with surveys, translucent symbols indicate estimates derived using integrated population modelling, fusing inferences of survival, reproduction and abundance, for years without surveys. Inset credit: A. Jearwattakanok.

adults in 2050. Extinction probability was estimated at $\hat{P}_e = 0.005$, assuming that current levels of temporal variability and habitat suitability extend into the future.

3.2 | Philopatry and metapopulation dynamics

The probability that a translocated Kuaka fledgling survived a translocation until fledging at the destination site was estimated at $\hat{\varphi}_T = 0.939$ (0.902–0.968; Appendix S1) based on data on congeners. Experts estimated the probability of juvenile Kuaka translocated to the destination returning to the source (return-to-source probability) at $\hat{\psi}_r = 0.297$ (0.024–0.725; Figure 4). Experts considered movements from the source to the destination unlikely for both adults and juveniles ($\hat{\psi}_{ad,S} = 0.019$; 0.0001–0.081 and $\hat{\psi}_{juv,S} = 0.045$; 0.001–0.158 respectively). Experts also considered movements of adults from the destination to the source unlikely ($\hat{\psi}_{ad,D} = 0.044$; 0.001–0.157), in contrast to movements of juveniles from the destination to the source ($\hat{\psi}_{juv,D} = 0.192$; 0.006–0.577).

3.3 | Vital rates at the destination

Experts considered it uncertain whether the candidate destination site (Rarotoka) was better or worse than the source (Whenua Hou), but on average predicted slightly lower adult survival and reproduction due to the presence of a larger suite of invasive plants and a potential native predator (Kelp Gull; *Larus dominicanus*) at the destination site ($\hat{\varphi}_{ad,D} = 0.853$; 0.749–0.931, $\hat{f}_D = 0.787$; 0.590–0.919, and

$\hat{r}_D = 0.639$; 0.472–0.786; Figure 5). Transforming the elicited distributions into coefficients gave $\hat{\beta}_{\varphi_{ad,D}} = -0.068$ (–0.700–0.566) for adult survival, $\hat{\beta}_{f_D} = -0.234$ (–1.183–0.721) for breeding probability and $\hat{\beta}_{r_D} = -0.079$ (–0.587–0.736) for breeding success. Maximum burrow density at the destination was considered highly uncertain, with an expert-elicited density of 0.081 (0.0003–0.423) burrows per m^2 , leading to a carrying capacity \hat{K}_D of 2002 (2–10,530) adults.

3.4 | Translocation scenarios

In all scenarios, translocation harvests caused a temporary reduction in source population size $\hat{N}_{ad,S}$, but harvests did not necessarily increase extinction probabilities at the source $\hat{P}_{e,S}$ (Figure 6; Table 1). All scenarios could result in potential establishment of a destination population, but extinction probabilities at the destination site $\hat{P}_{e,D}$ varied greatly. When ignoring effects of philopatry and metapopulation dynamics, higher harvest rates and timeframes increased harvest impact on $\hat{N}_{ad,S}$, but improved establishment success. When accounting for juveniles returning to the source post-translocation due to philopatry (i.e. including $\hat{\psi}_r$), both translocation impact and establishment success were reduced. Specifically, $\hat{N}_{ad,S}$ remained 6% larger when incorporating $\hat{\psi}_r$, while $\hat{N}_{ad,D}$ remained 27% smaller when incorporating $\hat{\psi}_r$. When accounting for full metapopulation dynamics, differences of translocation impact and establishment success in both \hat{N}_{ad} and \hat{P}_e under varying harvest intensities and timeframes disappeared as an equilibrium was reached between the two interacting populations. Regardless of effects of philopatry and metapopulation dynamics, the no-harvest scenario was stochastically dominant when considering either $\hat{N}_{ad,S}$ or $\hat{N}_{ad,total}$, while the most intensive harvest scenario was stochastically dominant when considering $\hat{N}_{ad,D}$ (Figure 7). However, despite differences at source and destinations under varying scenarios and metapopulation dynamics, overall extinction probabilities remained virtually equal.

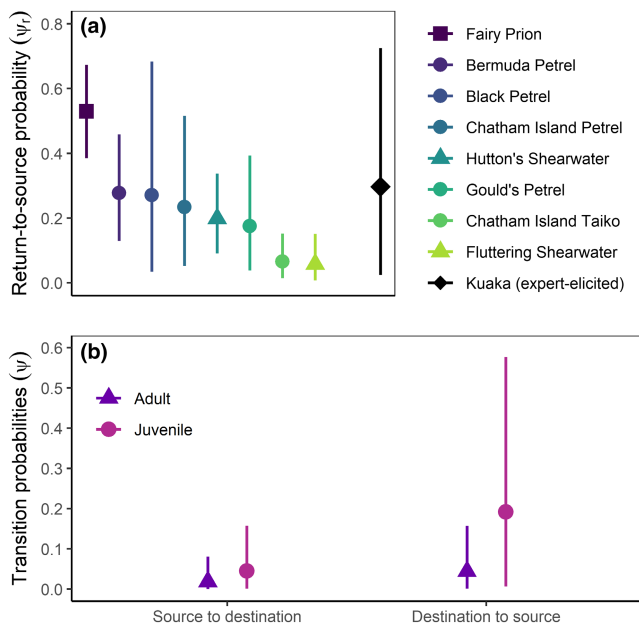


FIGURE 4 Estimates of return-to-source probabilities $\hat{\psi}_r$ for translocated juveniles of eight petrel species based on published data alongside the expert-elicited estimate for kuaka (a), and expert elicited probabilities of adult and juvenile kuaka moving between source and destination populations (b).

4 | DISCUSSION

We here show how to quantitatively and transparently assess the feasibility of translocations of Kuaka (Figure 1; IUCN, 2013), despite the extremely small size of the remaining population, the lower perceived quality of the potential destination site, the highly uncertain carrying capacity estimates, and the species' inherent philopatric and highly mobile nature. Our results show that establishing a second population of Kuaka is feasible, even in the face of these challenges. Establishing a second Kuaka population is considered highly desirable, as it would reduce long-term vulnerability of this species to storms, future climate change impacts, and other threats (i.e. conservation objectives; Fischer, Taylor, Cole, et al., 2020; Fischer, Wittmer, et al., 2021). Although not the focus of our study, successful (re)establishment of Kuaka would simultaneously reinstate lost ecosystem functioning at the destination site, providing wider benefits to dune systems in Aotearoa.

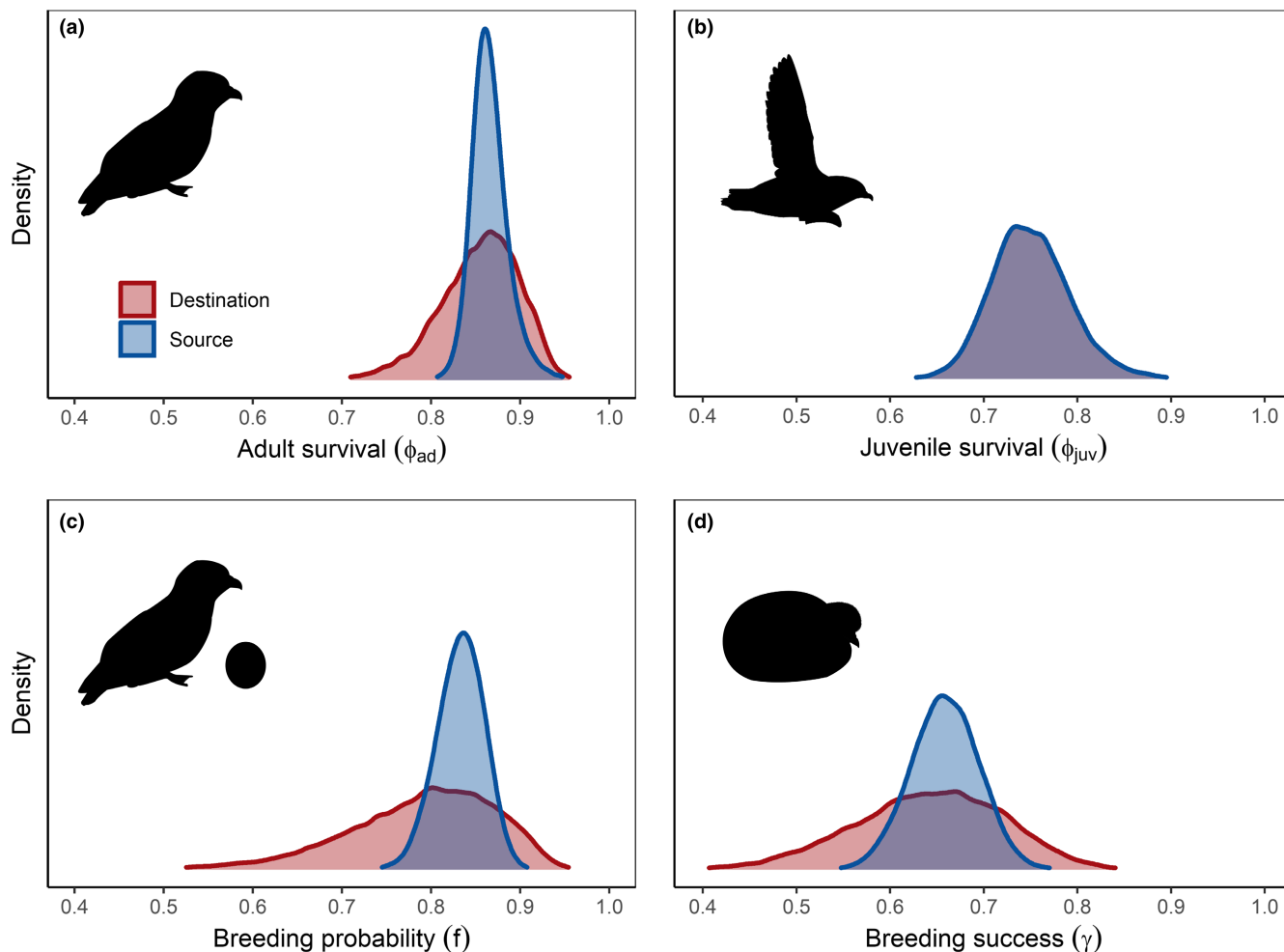


FIGURE 5 Kuaka adult survival (a), juvenile survival (b), breeding probability (c), and breeding success (d) at source (based on empirical data and integrated population modelling) and destination populations (expert-elicited). Juvenile survival was considered equal between the two populations due to the pelagic nature of this life cycle stage.

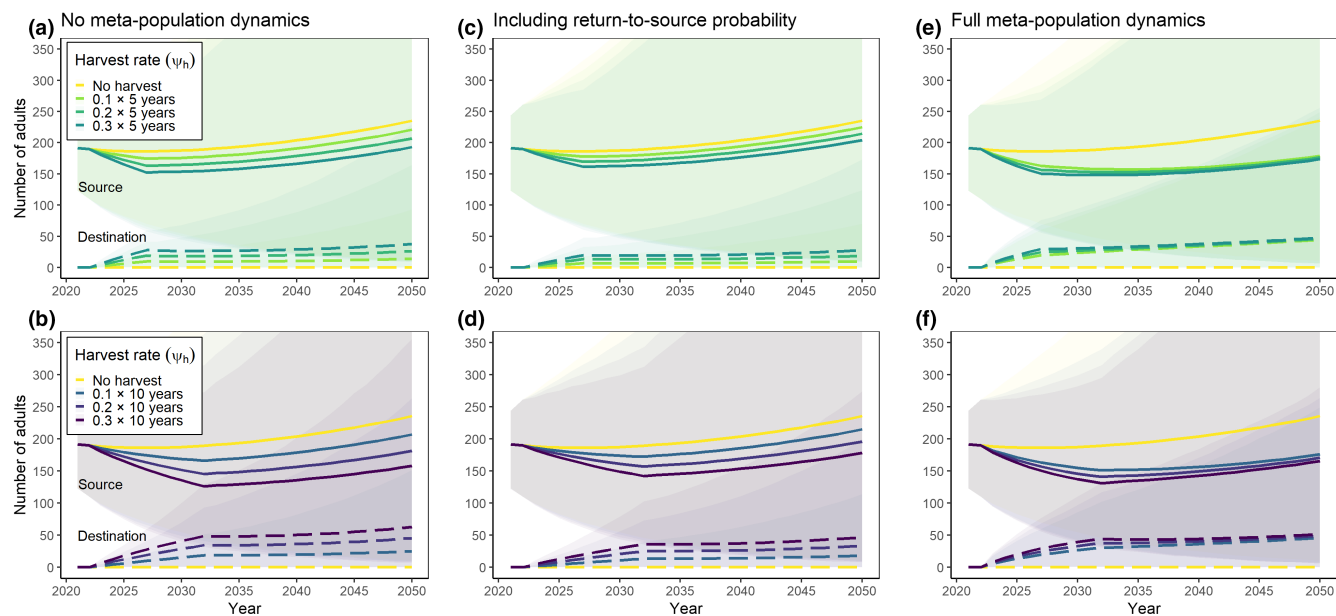


FIGURE 6 Estimated source (solid lines; $\hat{N}_{ad,S,t}$) and destination Kuaka population sizes (dashed lines; $\hat{N}_{ad,D,t}$) under various harvest intensities (0%–30% of all fledglings per year), harvest time frames (5–10 years) and metapopulation dynamics (no metapopulation dynamics (a,b), including return-to-source probability (c,d), and full metapopulation dynamics (e,f)).

TABLE 1 Estimated size of Kuaka source ($\hat{N}_{ad,S,t}$), destination ($\hat{N}_{ad,D,t}$) and total population sizes ($\hat{N}_{ad,total,t}$) with associated extinction probabilities (\hat{P}_e) in 2050 under varying translocation scenarios

Scenario		Outcome						
Harvest years	Harvest rate ψ_{ht}	Return-to-source probability $\hat{\psi}_r$	Metapopulation dynamics	$\hat{N}_{ad,S,2050}$	$\hat{N}_{ad,D,2050}$	$\hat{P}_{e,D,2050}$	$\hat{N}_{ad,total,2050}$	$\hat{P}_{e,total,2050}$
0	0			236 (11-896)	—	—	236 (11-896)	0.005
5	0.1			221 (10-845)	14 (0-93)	0.308	235 (11-889)	0.005
5	0.2			207 (10-788)	26 (0-164)	0.191	233 (11-881)	0.005
5	0.3			193 (9-736)	38 (0-229)	0.143	231 (11-884)	0.005
10	0.1			207 (10-792)	25 (0-151)	0.163	232 (11-881)	0.006
10	0.2			181 (8-694)	45 (0-263)	0.100	226 (11-869)	0.005
10	0.3			158 (7-600)	63 (0-355)	0.078	221 (10-863)	0.006
5	0.1	✓		224 (11-860)	10 (0-70)	0.404	236 (10-901)	0.006
5	0.2	✓		214 (10-819)	19 (0-124)	0.262	236 (9-898)	0.006
5	0.3	✓		204 (9-776)	28 (0-173)	0.198	235 (9-892)	0.006
10	0.1	✓		215 (10-820)	18 (0-114)	0.231	236 (9-892)	0.006
10	0.2	✓		196 (9-747)	34 (0-200)	0.140	232 (9-885)	0.006
10	0.3	✓		178 (8-681)	47 (0-274)	0.106	228 (9-877)	0.006
5	0.1	✓	✓	179 (7-699)	45 (0-241)	0.057	227 (9-870)	0.006
5	0.2	✓	✓	177 (7-693)	46 (0-249)	0.055	225 (9-872)	0.006
5	0.3	✓	✓	174 (7-679)	48 (0-256)	0.054	220 (9-831)	0.006
10	0.1	✓	✓	176 (7-688)	46 (0-249)	0.054	225 (9-867)	0.006
10	0.2	✓	✓	171 (7-670)	49 (0-264)	0.052	223 (8-869)	0.006
10	0.3	✓	✓	166 (6-652)	51 (0-280)	0.051	220 (8-858)	0.006

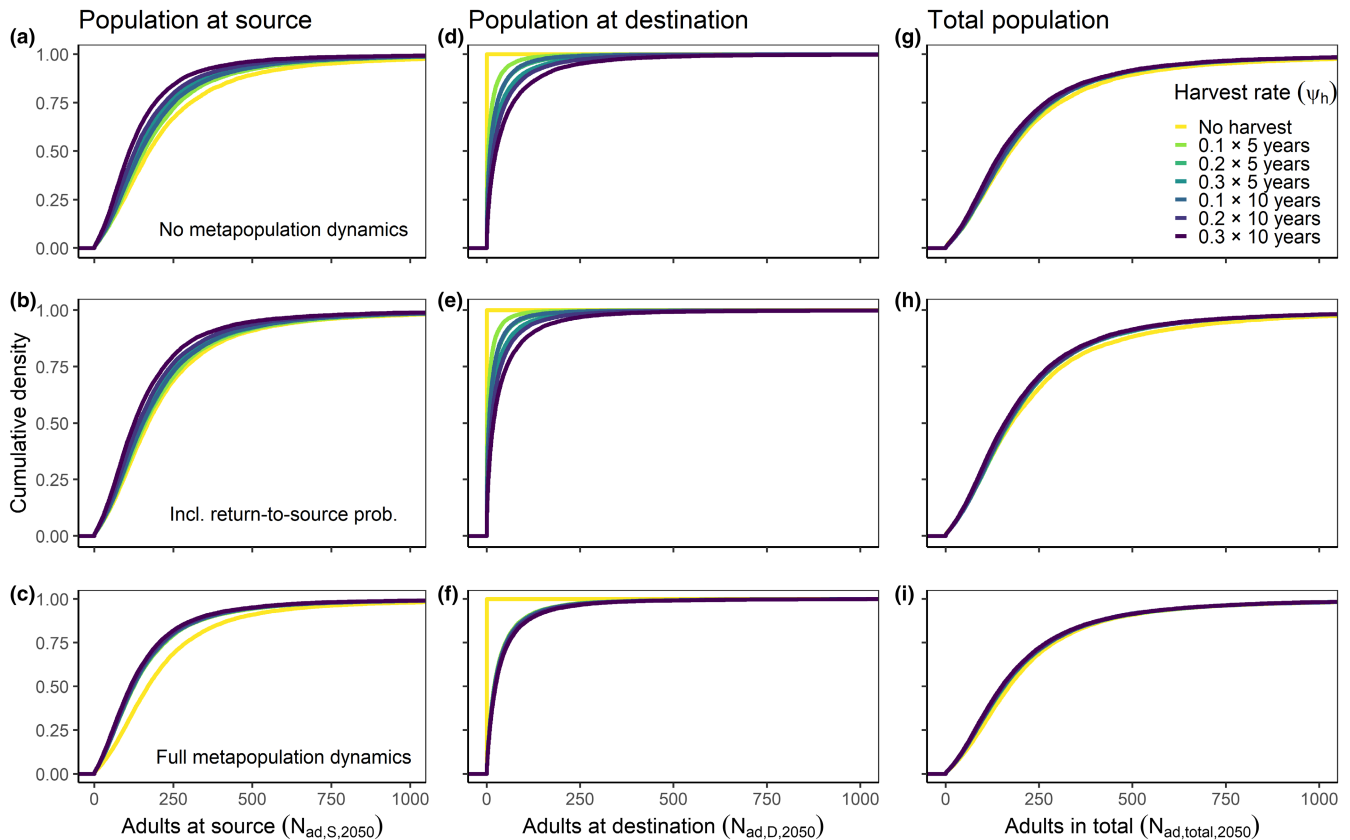


FIGURE 7 Cumulative density functions of projected source (a–c), destination (d–f) and total (g–i) kuaka populations in 2050 under various harvest intensities (0%–30% of all fledglings per year), harvest time frames (5–10 years) and metapopulation dynamics.

Our results emphasise that accounting for philopatry when planning translocations of mobile species is crucial (Oro et al., 2011; Ruffel & Parsons, 2009). For highly mobile seabirds, the potential of juveniles returning to source populations post-translocation is prevalent (e.g. Carlile et al., 2012; Miskelly et al., 2009) and can influence translocation impact and establishment success. We show that for Kuaka, failure to account for the return-to-source probability led to an overestimation of the destination population size by 27%, while simultaneously, harvest impact on the source was 6% lower. Therefore, elevated harvest intensities may be required to successfully establish destination populations of philopatric species. However, factors influencing philopatry remain poorly understood. Most seabird studies investigated the influence of the age of translocated fledglings and showed that birds should generally be harvested 2–6 weeks prior to fledging to minimise the return-to-source probability, which has now become common practice (e.g. Miskelly et al., 2009; Zhou et al., 2017). The influence of breeding biology, age of maturation, distance between source and destination, size of source and destination and social attraction systems have not been quantified and should be considered research priorities for future translocations of seabirds (e.g. Oro et al., 2011) and other mobile species (e.g. bats; Ruffel & Parsons, 2009).

Our results also highlight the importance of incorporating metapopulation dynamics post-establishment of a destination population when considering translocations of highly mobile species. In our study, juveniles recruiting from the destination to the source was

considered likely, creating the risk of the destination population ‘bleeding out’ following initial establishment (Oro et al., 2011). Yet, even with a low estimated transition probability, natural movements of adults from source to destination were sufficient to modulate the influence of different harvest intensities and high recruitment of juveniles from destination to source. Note that we treated transition probabilities as constant, when these probabilities are likely influenced by a range of factors that could vary over time, including the population size of source and destination, or the use of social attraction systems (Miskelly et al., 2009; Miskelly & Taylor, 2004; Oro, 2020). Despite their potential importance, impacts from metapopulation dynamics on translocation outcomes are even less often investigated than impacts from philopatry and should therefore also be considered a research priority (Oro et al., 2011).

As with all conservation actions (Soulé, 1985), translocations are value-driven, and as such, the appropriate translocation protocols, balancing harvest impact and establishment success, are dependent on underlying values. Our results show that if minimising impact on the source or maximising overall population size is the sole objective, a no-harvest scenario would be the preferred option. Translocations come with risks (IUCN, 2013), which we modelled explicitly. Consequently, our results show that reductions in population size at the source, as well as slight reductions in the overall population size following translocations should be anticipated. However, if maximising establishment

success is the sole objective, the most intensive harvest scenario would be the preferred option. In reality, source, destination and overall population size will all be important objectives to consider. Therefore, finding the right harvest intensity and timeframe will rely on explicit expression of underlying values (Panfylova et al., 2019). To incorporate these underlying values and identify the right balance appropriately, decisions on translocation protocols should be subjected to structured decision-making frameworks (Converse et al., 2013; Gregory et al., 2012). Such frameworks would allow the consideration of other fundamentally important values (e.g. Indigenous value systems or costs) in a meaningful way (Figure 1; McMurdo Hamilton et al., 2021). The study reported here is part of such a structured decision-making process, and in combination with the objectives expressed by the participants, has provided the biological information necessary to decide on the best course of action for the Kuaka (Fischer, Parker, et al., 2022).

Conservation translocations of endangered, philopatric, highly mobile species are challenging, yet these interventions are also crucial for the future of these species (e.g. Carlile et al., 2012; Miskelly et al., 2009; Oro et al., 2011), and as such need careful feasibility assessments (IUCN, 2013). We here use state-of-the-art approaches, combining novel metapopulation IPMs with expert elicitations through a user-friendly app, to quantitatively assess the feasibility of such translocations. We illustrate that once biological and other fundamental values placed on source, destination and overall populations are expressed explicitly (Panfylova et al., 2019), the appropriate Kuaka translocation protocol can be identified and implemented. In summary, our study illustrates that the feasibility of these extremely challenging and risky translocations can be assessed quantitatively and transparently, which will facilitate better decision-making in the future than conventional qualitative approaches (IUCN, 2013).

AUTHORS' CONTRIBUTIONS

J.H.F. conceived the research and led the writing of the manuscript; J.H.F., H.U.W., R.C., I.D., G.A.T. and D.P.A. collected the data; J.H.F., C.F.K. and D.P.A. analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data and code are available from the New Zealand Department of Conservation (<https://birdbanding.doc.govt.nz/>) and the Dryad Digital Repository <https://doi.org/10.5061/dryad.pk0p2ngqq> (Fischer, Wittmer, et al., 2022).

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SUPPORTING INFORMATION

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