New Zealand Journal of Ecology (2022) 46(1): 3454 © 2022 New Zealand Ecological Society.

NEW ZEALAND JOURNAL OF ECOLOGY

REVIEW

Kiwi translocation review: are we releasing enough birds and to the right places?

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Published online: 13 September 2021

Abstract: Translocations of kiwi (*Apteryx* spp.) are one of the most common and growing types of conservation translocations in New Zealand. However, their outcomes remain mostly unpublished, which does not allow for sharing of lessons learnt from past developments. We reviewed 102 kiwi translocations from the 19th century until 2018, and identified factors affecting their outcome. North Island brown kiwi (*A. mantelli*) was the most translocated species, but the highest impact of translocations on the improvement of conservation status was for the rarest taxa: little spotted kiwi (*A. owenii*), rowi (*A. rowi*), and Haast tokoeka (*A. australis* 'Haast'). Translocations are typically used for creating secure populations and, more recently, for ecosystem restoration objectives and meta-population management. We developed a set of criteria to evaluate the outcome of introductions and reintroductions based on demographic parameters alongside current recommendations on genetic make-up of translocated populations. These criteria allowed us to categorise historical and recent translocations that were carried out for a wide array of objectives. Currently, based on these criteria, only a few translocated populations can be considered successful in the medium–long term: 15+ years following the release of a genetically diverse population (40+ unrelated individuals). Most historical translocations failed or require further genetic and habitat management. However, a majority of kiwi translocations have occurred over the last two decades and, while several populations have successfully established, for most of them, it is too soon to assess their medium-long term outcome. An analysis of factors affecting translocation outcomes revealed that, despite ongoing predator control, populations at small, unfenced sites on the mainland suffer from dispersal and predation, which has negative demographic and genetic consequences. Releases to larger mainland sites and predator-free areas have increased survival times, which indicates higher chances for a positive translocation outcome. Moreover, translocated wild-caught and captive-sourced birds survived longer compared to birds from the Operation Nest Egg programme, particularly at sites that were not predator-free. We highlight the need for genetic considerations in the planning and adaptive management of proposed and existing translocated populations. Specifically, we suggest that differences in kiwi survival, based on the type of released birds and release site's area size and predator status, should be considered during translocation planning. Similarly, we encourage a standardised monitoring approach, increased reporting, and publishing the outcomes of translocations.

Keywords: *Apteryx*, conservation translocation, post-release effects, post-release survival, reintroduction, reinforcement, translocation outcome, translocation success

Introduction

Wildlife translocations, together with pest eradications, are perceived as achievements of conservation management in New Zealand. These management tools have built upon years of lessons from initial "trial-and-error" efforts (Brichieri-Colombi & Moehrenschlager 2016). Kiwi management over the past hundred years illustrates this evolution of New Zealand conservation, and its understanding helps us to advance the use of reintroduction biology in practical management.

Around the turn of the 19th century, kiwi translocations were reactive measures to save populations from the imminent threat of predation (Armstrong et al. 2015) or habitat loss due to logging in the second half of the 20th century (Colbourne 2005). Early transfers between mainland sites were mostly unsuccessful as most or all birds died or dispersed (Saunders 1995; Miskelly & Powlesland 2013), but many early translocated island populations have persisted until the present (Colbourne & Robertson 2000). Advances in pest eradications on islands (Armstrong & McLean 1995),

DOI: https://dx.doi.org/10.20417/nzjecol.46.1

landscape-scale predator control (Saunders & Norton 2001), and fenced sanctuaries have allowed successful releases of kiwi and other wildlife valued by communities throughout New Zealand (Burns et al. 2012; Smuts-Kennedy & Parker 2013; Innes et al. 2015a). Those advances in predator control techniques, mainly trapping and poisoning, have led to the creation of larger ecosystem restoration areas (Saunders & Norton 2001; Innes et al. 2019), which also enabled effective management of remnant kiwi populations in situ.

Kiwi are the most translocated bird species in New Zealand (Cromarty & Alderson 2013; Miskelly & Powlesland 2013) and the number of new projects and released birds are steadily increasing. Originally, all translocated kiwi populations were sourced from existing wild populations. However, in 1995, Operation Nest Egg (ONE), a new method of intensive management of kiwi, was developed to source birds to supplement existing populations or to establish new populations. Operation Nest Egg involves removing kiwi eggs from the wild, incubating and hatching chicks in a captive facility, and keeping them in a predator-free environment (crèche) until they reach a safe size (typically 0.8–1.2 kg) to fend off stoats (*Mustela erminea*), before releasing them back into the wild (Colbourne et al. 2005; Gillies & McClellan 2013). This method has been widely used for several kiwi species (Innes et al. 2015b). Initial successes of these developments and increased involvement of community groups, iwi and hapū, resulted in a boom of kiwi translocations over the last two decades. As the number of translocations grew, so did the translocation objectives. The objectives vary: creating secure populations and establishing kōhanga sites/source populations to supply wild kiwi for releases elsewhere (Innes et al. 2016), meta-population management (Robertson et al. 2019a), ecosystem restoration projects (Innes et al. 2019), and mitigation transfers (Colbourne & Robertson 2000).

There is a lack of information on kiwi translocations and their outcomes, which makes it difficult to assess overall translocation effectiveness, address possible issues, improve translocations as a tool, and identify the role that translocations play in kiwi recovery management. Currently, there is no database of all kiwi translocations, and the existing registers lack sufficient detail to fully document the scope of translocations and objectives for which they were carried out. Outcomes of translocations remain mostly unpublished and are often unreported, especially for those that failed or had uncertain outcomes (Fischer & Lindenmayer 2000; Miller et al. 2014; Gitzen et al. 2016).

A thorough assessment of translocations is critical for the refinement of this management tool (Brichieri-Colombi & Moehrenschlager 2016) to maximise the probability of positive outcomes (Batson et al. 2015). Here we review the information from kiwi translocations with a focus on the last four decades. Specifically, we assess the level of translocation effort for each taxon and the evolution of translocation objectives over time. Additionally, we evaluate translocation outcomes and investigate contributing factors, such as source type of released birds and predator status at the release site. Finally, we identify issues with the past and current practice and provide recommendations addressing the issues faced by the translocation projects in accordance with the latest Kiwi Recovery Plan (Germano et al. 2018).

Methods

Definitions and terminology

Translocations are intentional movements of wildlife by humans from one place to another and are often used in conservation management (Seddon 2010; Seddon et al. 2014). To qualify as a 'conservation translocation', the aim of the movement should be to produce a measurable conservation benefit at a population, species, or ecosystem level. Other types of translocations are carried out solely to benefit the translocated individuals, such as mitigation translocations and rehabilitation releases, or for aesthetic reasons/enjoyment by landowners (IUCN/SSC 2013). In recent decades, translocations have been also carried out for conservation advocacy and community interest (Parker 2008).

We separate conservation translocations into 'conservation introductions', releases of species or particular taxa outside their historical range, and 'population restorations', releases within their range: an area in which the taxon naturally occurs or was known to occur in the past (IUCN/SSC 2013). Additionally, we discern between two types of population restorations. First, a 'reintroduction' happens where a species has become locally extinct. Second, a 'reinforcement' (alternatively 'supplementation') happens when a population of the species is still present at the release site (Seddon et al. 2012). We also differentiate between two types of conservation introductions based on their purpose. First, 'assisted colonisation' aims to create a secure population to avoid species extinction. Second, 'ecological replacement' allows the translocated species to fulfil an ecological function of a previously extinct taxon (Seddon et al. 2012). Translocations can consist of a single release or can take place over several years and consist of multiple releases until the desired number of translocated animals is achieved (Griffith et al. 1989).

Data collection

We collated a dataset of 102 kiwi translocation projects that occurred between 1863 and 2018 from a large variety of sources, which included: the Department of Conservation's translocation register, the Zoo and Aquarium Association's brown kiwi studbook, published reviews and summaries (Atkinson 1990; McHalick 1998; Colbourne & Robertson 2000; Colbourne 2005; Miskelly & Powlesland 2013), websites "Reintroduction projects in New Zealand" (www.massey.ac.nz/~darmstro/nz_projects.htm) and "Avian Reintroduction & Translocation" (www.lpzoosites.org/artd/; both accessed in July 2020), journal articles, published and unpublished reports, translocation proposals, management plans, monitoring data and various relevant information provided by project managers and associates. Historical translocations were typically poorly documented, or the documents were difficult to locate and access. For that reason, we generally focused on the 76 translocations occurring in the last four decades (1979–2018), with an emphasis on the 60 translocations from the last two decades (1999–2018), for which post-release monitoring data and supplementary information were more available.

We reviewed all conservation translocations but also included mitigation translocations, rehabilitation releases (if these were supplementary to a wider kiwi conservation project), and other known historical translocations. Some of these projects extend beyond the conservation translocation spectrum (Seddon 2010; IUCN/SSC 2013), but we included them in the dataset to have a complete picture of the use of kiwi translocations in New Zealand. Specifically, we included all translocations of wild birds, birds from captive facilities, and intended permanent releases of juveniles and subadults from the ONE programme, provided that these birds were released at a location different to their source site. In contrast, temporary translocations of ONE birds to a crèche site, ONE releases to the original source population, transfers to captivity, and other releases not intended to found a permanent kiwi population were excluded from our review. Releases of different kiwi species to a single site were treated as separate translocation projects. Also, translocations of the same species into the same site were treated as separate projects if there were more than 15 years between the releases and therefore were unlikely a part of the same series of releases.

To enable a thorough analysis of the translocation information, we recorded various parameters for each translocation and, where possible, for each release event within a translocation. The parameters included: taxon; year; release site and its area size and type (mainland, island, fenced sanctuary); source site; founder source type (wild, captive, ONE); number of released birds; post-release survival; how many birds dispersed and attempted to breed; type of monitoring (radio-telemetry, call counts, recapture); length of monitoring; presence and type of introduced mammalian predator control; translocation objective; and lead entity (DOC, community group, iwi/hapū). For translocations to islands and fenced sanctuaries, the whole area of an island or a sanctuary was considered as the translocation project area. At mainland unfenced sites, the project area was equivalent to the size of the area under predator control, in which the released birds were expected to settle. At sites with no predator control, the size of a reserve or another designated protected area where the kiwi were released, was considered as the project area. Where additional predator control buffer zones were created around the project area, such zones were not deemed part of the project area, as their main purpose was to reduce the probability of predator incursions rather than for the birds to settle in them.

The geographic scope of original species ranges and kiwi taxonomy were based on the current state of knowledge as described in Weir et al. (2016), Shepherd et al. (2012), and Germano et al. (2018). All taxa or evolutionarily significant units of brown kiwi (*A. mantelli* – Northland, Coromandel, Western, Eastern) and tokoeka (*A. australis* – Haast, North Fiordland, South Fiordland, Rakiura) were analysed separately. Great spotted kiwi/roroa (*A. haastii*), little spotted kiwi (*A. owenii*), and rowi (*A. rowi*) were each treated as a single taxon unit because they have been managed as such. All translocations to islands, where kiwi had not been recorded before, were considered as introductions, similar to Seddon et al. (2015). Only early translocations of tokoeka to Resolution Island (1895–1898), little spotted kiwi to Cooper Island (1903), and brown kiwi to Te Hauturu-o-Toi/Little Barrier Island (1903–1919) were considered reinforcements due to presumed naturally-occurring populations still there at the time (Henry 1895; Palma 1991; Colbourne 2005).

Assessing translocation outcomes

Evaluating translocation outcome is challenging because there is no scientific consensus on what constitutes translocation success (Chauvenet et al. 2013; Robert et al. 2015). Success criteria generally depend on the set objectives and type (e.g. reintroduction vs reinforcement) of each particular translocation (Armstrong et al. 2019). Moreover, most reported outcome evaluations focus on the establishment phase of a translocated population. However, even though successful establishment and growth are necessary for a population to be viable in the long-term, they do not predict the ultimate translocation outcome (Robert et al. 2015). Therefore, to accurately evaluate translocations, we need to distinguish between three post-release phases: population establishment, growth, and self-regulation (Sarrazin 2007; Armstrong & Seddon 2008).

Assessing and comparing the outcomes of kiwi translocations is further challenged by kiwi life-history and ecology. Several decades may be required before a translocated population reaches the regulation phase and so be considered as successfully persisting for the long term, over multiple generations. All kiwi species are long-lived with a possible life expectancy exceeding 50 years for most taxa (Heather & Robertson 2015). Kiwi are irregular breeders and require 1–5 years before they reach sexual maturity, with variation among the taxa (Heather & Robertson 2015). All kiwi are sexually dimorphic, which allows for relatively simple sexing of adults in the field, but it is not possible to reliably assign age once mature (McLennan & McCann 1993; Robertson & Colbourne 2017). These characteristics make it difficult for long-term monitoring of translocated populations consisting of unmarked individuals.

We based our assessment of translocation outcomes on the assumption that the primary objective of most translocations is to establish or restore a population with a high probability of persistence (Converse & Armstrong 2016). Such populations require sustained population growth (Armstrong & Reynolds 2012) and an adequate number of founders to minimise the loss of genetic diversity (Weeks et al. 2015). This objective aligns with the main recovery goals for kiwi management: grow populations of all species by at least 2% per year and maintain their genetic diversity (Germano et al. 2018). To achieve sufficient retention of genetic diversity, at least 40 unrelated individuals of brown kiwi need to be released initially (Weiser et al. 2013; Weiser 2014). This number of starters (initially released birds) is expected to maximise the probability of persistence and avoid genetic deterioration of introduced populations (Weeks et al. 2015; Frankham et al. 2017). The target of releasing 40 individuals to a project area with a carrying capacity for at least 100 pairs was adopted for all kiwi taxa by the official Department of Conservation guidelines (Sporle 2013; Robertson & Colbourne 2017; Department of Conservation 2018), and we included it among the criteria for a successful introduction or reintroduction in this review. We excluded reinforcements from the outcome assessment given that it was not usually possible to attribute the contribution of the released individuals to population growth or genetic diversity.

Assessment of the translocation outcome is based on the point in time when the assessment was made, and hence it may change subsequently (Wolf et al. 1996; Seddon 1999). We set the minimum assessment timeframe of 15 years to allow a sufficient period for the population to start growing following the post-release effects and acclimation period of suppressed growth rate (Converse & Armstrong 2016). This window leaves out populations in the establishment phase, but allows assessment of projects in the growth and regulation phases. Armstrong and Reynolds (2012) and Robert et al. (2015) argue that the ultimate evaluation of translocation success should happen only once an introduced population reaches carrying capacity. Nonetheless, populations at different sites and of different taxa reach carrying capacity at different times, and so, for practical reasons and for the ability to compare the projects, we chose an intermediate duration of 15 years. This 'in progress' period was expected to provide enough time for the released juveniles or subadults of all taxa to mature and breed, as well as for their offspring to start breeding. This timeframe provides a reasonable indicator of success in the population growth phase without requiring data across the decades that may be necessary to reach the regulation phase at all sites.

Translocation outcome definitions

We divided translocation outcomes of introductions and reintroduction projects into five categories, which are similar to the categories used in reviews by Miskelly and Powlesland (2013) and Brichieri-Colombi and Moehrenschlager (2016):

Likely successful: a successfully established population growing at least 2% on average per annum (finite rate of increase) over a minimum of 15 years, after 40+ individuals were released. Also, self-regulating populations of 100+ pairs founded by 40+ individuals. Further immigrants likely need to be periodically added or immigration facilitated for maintaining genetic diversity.

Requiring further management: an established population 15+ years after the latest release with less than 40 released birds in total, which will likely require more major releases or ongoing genetic management. Also, populations below the 2% average annual growth rate and kōhanga sites, more than 15 years since the latest release.

In progress: a population less than 15 years since 40+ birds were released or a population with less than 40 birds released within the last 15 years.

Unsuccessful: a population showing signs of decline below 50% of the initially released birds at 15+ years post the latest release, or in cases where released birds were removed from the project area.

Not assessed: a reinforcement translocation or an introduced hybrid population of individuals originating from different kiwi species.

Data analysis

Project-level analysis

First, we carried out an exploratory analysis of translocation projects and how they evolved. Specifically, to assess the trends in numbers of new translocations in each decade, we plotted individual projects using decadal bins. Similarly, to display trends in the type of release sites over time, we binned the numbers of all translocated birds in one-year intervals. To explore translocation effort for each taxon over the last 40 years, we plotted the numbers of translocated birds and translocation projects and compared the number of translocated birds in this period with 2018 populations estimates (Germano et al. 2018). To inspect the geographic distribution of translocations, we plotted central points of project areas onto a map of New Zealand. Because some projects areas were either close to each other or overlapping, we plotted the points with a jitter factor of 0.01 arc degrees. Subsequently, we compared source types of translocated birds by displaying numbers of released individuals for each species based on their origin (wild-caught, captive, ONE). Then, we evaluated the habitat type and size of project areas. To assess the evolution of motivations for translocations, we compared primary and secondary objectives for periods before-and-after 1989 to highlight the shift of dominant objectives in the last three decades. Finally, we estimated proportions of translocations led by different entities and based on reporting in the literature.

In the following step, we assessed outcomes of translocations and assigned them into the categories, as mentioned above. Following this assessment, we carried out a sensitivity analysis to categorise translocations with adjusted criteria using three different values for numbers of released birds (35, 40, 50) and three different assessment timeframes (10, 15, 20 years). This step enabled us to evaluate how variation in the criteria threshold affects the number of likely successful translocations.

Individual-level analysis

Subsequently, we explored how different characteristics of translocation projects affect the survival of released birds. Initially, we assessed differences in the magnitude of post-release effects, specifically mortality and dispersal. Then, we modelled mean survival times based on translocation characteristics. We used a set of Bayesian time-to-event generalised mixed effect models. The response variable of the model was the survival time of the released birds in the project area. We used a Bayesian approach for three main reasons. First, Bayesian models have been shown to be better suited to deal with small sample sizes similar to those in our dataset, and therefore ideal for modelling translocated populations (Chauvenet et al. 2015). Second, the flexibility of Bayesian models allowed incorporating random effects in a time-to-event regression framework. Third, and most importantly, this approach enabled us to better understand the uncertainties of the model estimates.

To fit the model, we used the R package brms 2.14.4 (Bürkner 2017). We used a normal prior ($\mu = 0$, $\sigma = 5$) for all the population-level effects and an exponential prior ($\lambda = 1$) for our response variable. We used four independent Markov chains (Hamiltonian Monte Carlo algorithm) with 5000 iterations each. Trace plots of all Markov chains suggested model convergence and Gelman and Rubin's potential scale reduction factor $\hat{R}$ for all model estimates was below 1.002.

Data on post-translocation survival in the project areas was available in most cases for at least a subset of the released birds in projects since 1979. We also included rare cases of known survival from incidental reports before 1979 (six projects) and reports of local extinctions from failed translocations. The exact survival time of translocated birds was usually unavailable, and therefore our response variable was structured as a range of minimum and maximum possible survival times. The range of possible survival times was determined for 41% of the translocated birds. Often the time ranges were large, but they still provided valuable information about the differences between the translocation characteristics.

For those birds from all taxa for which we were unable to determine maximum possible survival time, we used a value of 50 years, in line with the estimated life expectancy of several kiwi species (Heather & Robertson 2015). For instance, the survival information of 10% of the birds was available only for the full first 12 months post-release after which monitoring stopped, or data were unavailable. Therefore, the exact survival time for these individuals could be anywhere between 1–50 years. These ranges were included as censoring intervals in our time-to-event model. We modelled the survival ranges using a log-normal family distribution. This distribution assumes a constant hazard rate and is commonly used to model time-to-event data when the rate of the event peaks at intermediate levels of the expected lifetime.

In the model, we included five variables as predictors of the mean survival time of translocated birds, two of them as fixed effects and three as random effects. As fixed effects we included the factors where we more expected their potential impact on management decisions: 1) the source type of the translocated birds (either wild, ONE, or captive), 2) the predator status (either predator-free, predator-managed by trapping/poisoning/both, or predator-present and not managed). We separated sites with predator management into two groups based on area size under predator control delimited by the median area for mainland unfenced sites. As random effects we included: 1) the kiwi taxon, 2) the translocation project, and 3) whether the birds were part of an introduction/reintroduction or a reinforcement translocation. Although this last predictor could have been also included as a fixed effect, we decided to model it as a random effect because later releases of an introduction/reintroduction project may resemble a reinforcement project and hence it was not always possible to unequivocally categorise individual releases. Including the translocation type as a random effect allowed us to account for the variability around this factor without the challenges of interpreting model estimates for each of the two translocation types. Subsequently, we tested for differences within our explanatory variables and presented the strength of evidence based on posterior probability. At mainland unfenced sites, birds were considered to have survived if they remained in the project area to act as population founders. Birds dispersing outside the project area were assumed to be unlikely to breed successfully due to limited or no predator control. However, birds that dispersed and subsequently returned to the project area, or birds that were brought back by managers and then stayed, were considered to have survived.

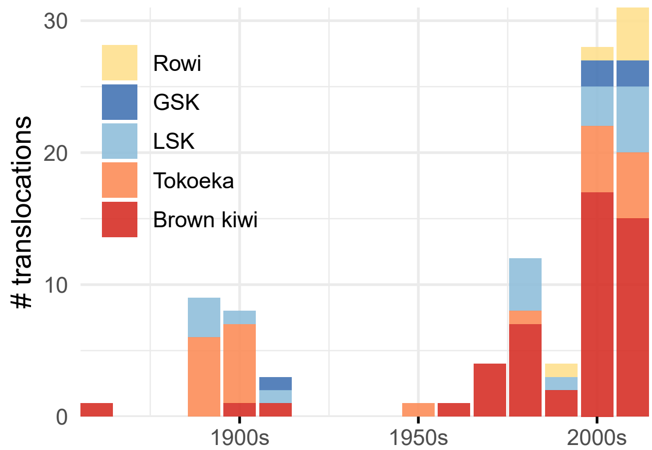

Figure 1. Numbers of kiwi translocation projects between 1860–2018 (n = 102). Project numbers increased rapidly in the last two decades. Projects were assigned to the decade in which they started. First recorded translocation was in 1863, the last in December 2018. Each colour represents a different kiwi species: rowi, great spotted kiwi (GSK), little spotted kiwi (LSK), tokoeka, and brown kiwi. Projects marked as rowi in the 1990s and 2000s show translocations of LSK/rowi hybrids, while in the 2010s only translocations of rowi occurred.

Results

Number of translocations and translocated birds over time

We identified 102 translocation projects that occurred between 1863 and 2018 (Fig. 1). It was not always possible to establish the numbers of released birds, particularly for the historical translocations. However, we were able to determine that at least 2572 birds were translocated through the end of 2018 (Fig. 2). After the initial wave of translocations in Fiordland at the turn of the 19th century and releases to Kapiti and Te Hauturu-o-Toi/Little Barrier islands in the early 20th century, there was little such activity until the 1970s. From then on, the number of new projects has generally been increasing every decade. The highest increase of translocation events and the number of translocated birds occurred during the last two decades, with 76% of all translocated kiwi released in the last 15 years (2004–2018).

In the period 1979–2018, for which we have the most information, 76 translocation projects were carried out. These projects took place over five years on average (range: 1–17 years), and in many cases, releases are likely to continue. For the same period, we recorded at least 817 separate release events (releases on consecutive days were counted as a single event). The median number of release events per translocation was four (1–73), with the overall length and number of releases increasing markedly in the last two decades. The median number of released individuals per project was 25 birds (1–169, n = 74; two projects with missing and incomplete data were not included). The median number of released birds for introduction and reintroduction projects was 29 (2–169, n = 53), while for reinforcements it was 11 (1–114, n = 21). The sex ratio of adult males to females was 1.1:1, the reporting on age classes was highly inconsistent among the projects.

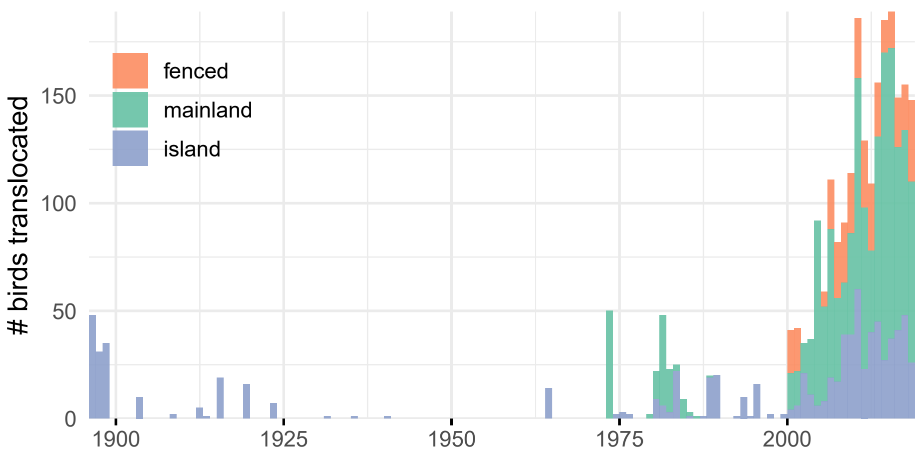

Figure 2. Numbers of translocated birds for different release site types between 1895–2018 (n = 2572). Numbers of translocated birds show a steady increase since 2000. Each colour represents a different type of release site: fenced sanctuaries (ring- or peninsula-fenced), unfenced mainland sites, and islands. Information about numbers of released birds from several translocations before the 1990s may be incomplete or missing; numbers of birds released before 1895 are unknown.

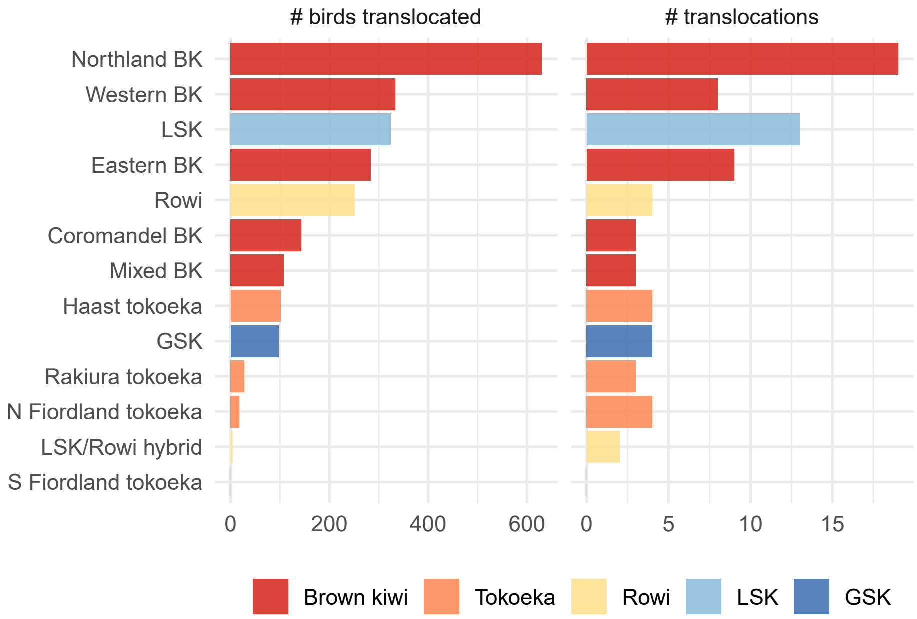

Figure 3. Numbers of translocated birds and translocation projects by kiwi taxon between 1979–2018. Brown kiwi, particularly the Northland taxon, were most translocated taxa, whereas the populous South and Stewart Island taxa were least translocated. Each bar represents either a different species: little spotted kiwi (LSK), rowi, great spotted kiwi (GSK), or a taxon/ evolutionarily significant unit of brown kiwi (BK): Northland, Western, Eastern, Coromandel, and mixed brown kiwi of various origin, or tokoeka: Haast, Rakiura, North Fiordland, and South Fiordland. No South Fiordland tokoeka releases were recorded during this period. Each colour represents a different kiwi species, LSK/rowi hybrids are displayed in the same colour as rowi.

In this period, most translocation projects (55%) were of brown kiwi, followed by little spotted kiwi (17%), tokoeka (14%), great spotted kiwi (5%), rowi (5%), and hybrids of rowi and little spotted kiwi (3%) (Fig. 3). Proportions of translocated birds relative to the current (2018) total population estimates differed considerably among kiwi taxa (Fig. 4). The rarest taxa, rowi and Haast tokoeka, together with little spotted kiwi, had the highest percentage of translocated birds in the last four decades. All brown kiwi taxa also had substantial proportions of translocated birds relative to their total populations, while for more populous South and Stewart Island taxa less than one per cent of their extant populations were translocated birds.

The spatial pattern of translocations

The geographic distribution of kiwi translocation projects

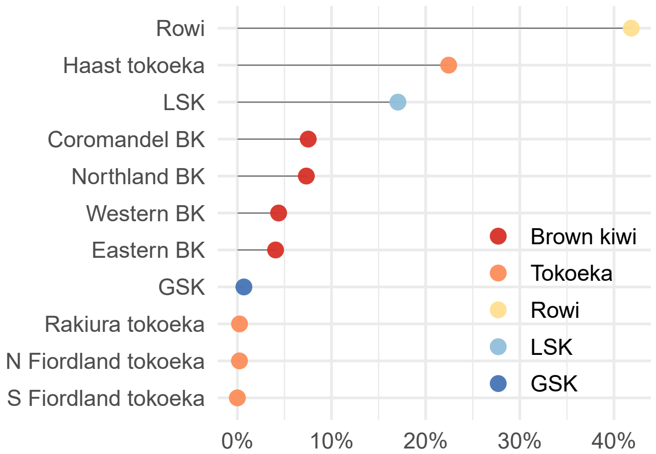

Figure 4. Percentages of translocated birds between 1979–2018 relative to the 2018 population estimates for each kiwi taxon (Germano et al. 2018) indicating translocation effort. For the three rarest taxa, the share of translocated individuals relative to their overall populations was the highest, whereas, for the populous South and Stewart Island taxa, the share of translocated individuals was less than 1%. Taxa as in Figure 3; hybrids and mixed provenance brown kiwi translocations are not included.

was unevenly spread across New Zealand. Since the 1860s, most of the release sites (63%) were in the North Island, or the surrounding offshore islands. Only 33% and 4% of all translocations were to South and Stewart Island sites, respectively (Fig. 5). Most of the release sites (86%, n = 87) were unique to a single kiwi translocation project. However, 12 release sites received birds as part of two or three different translocation projects, with seven of those receiving at least two different species. Resolution, Long, and Anchor islands in Dusky Sound, Fiordland, had both tokoeka and little spotted kiwi released on them in the late 19th century. Even though little spotted kiwi had not persisted at any of those sites, the species was re-released on Anchor Island in 2015. Kapiti and Te Hauturu-o-Toi/Little Barrier islands both received three kiwi species in the early 20th century. At Kapiti Island, little spotted, brown kiwi, and tokoeka were released, but only little spotted kiwi thrived there, while just a small population of likely brown kiwi and tokoeka hybrids remain on the island (Colbourne 2005). At Te Hauturu-o-Toi, brown, great spotted kiwi, and probably a single tokoeka were released, but only brown kiwi persisted. Mana Island first held a small hybrid population of rowi and little spotted kiwi, which was later removed, before the island received rowi two decades later. Among the recent projects, only Cape (Kidnappers) Sanctuary has two kiwi species – brown and little spotted kiwi, which are held separately. Brown kiwi were introduced to Mokoia Island for the second time after a previously failed attempt. The remaining four island projects (Motukawanui, Tiritiri Matangi, Red Mercury, and Ulva) released kiwi to supplement previously introduced populations.

Translocation type

Most kiwi translocations (58%) were introductions to places where the kiwi taxa were not known to occur previously, such as on offshore islands, or to areas on the mainland outside of their historical range. Reintroductions (within the historical range) accounted for only 19% of all translocation projects. Finally, 24% of all translocations were reinforcements of either naturally existing populations, or, in four cases, populations that were previously established by earlier introductions (see above).

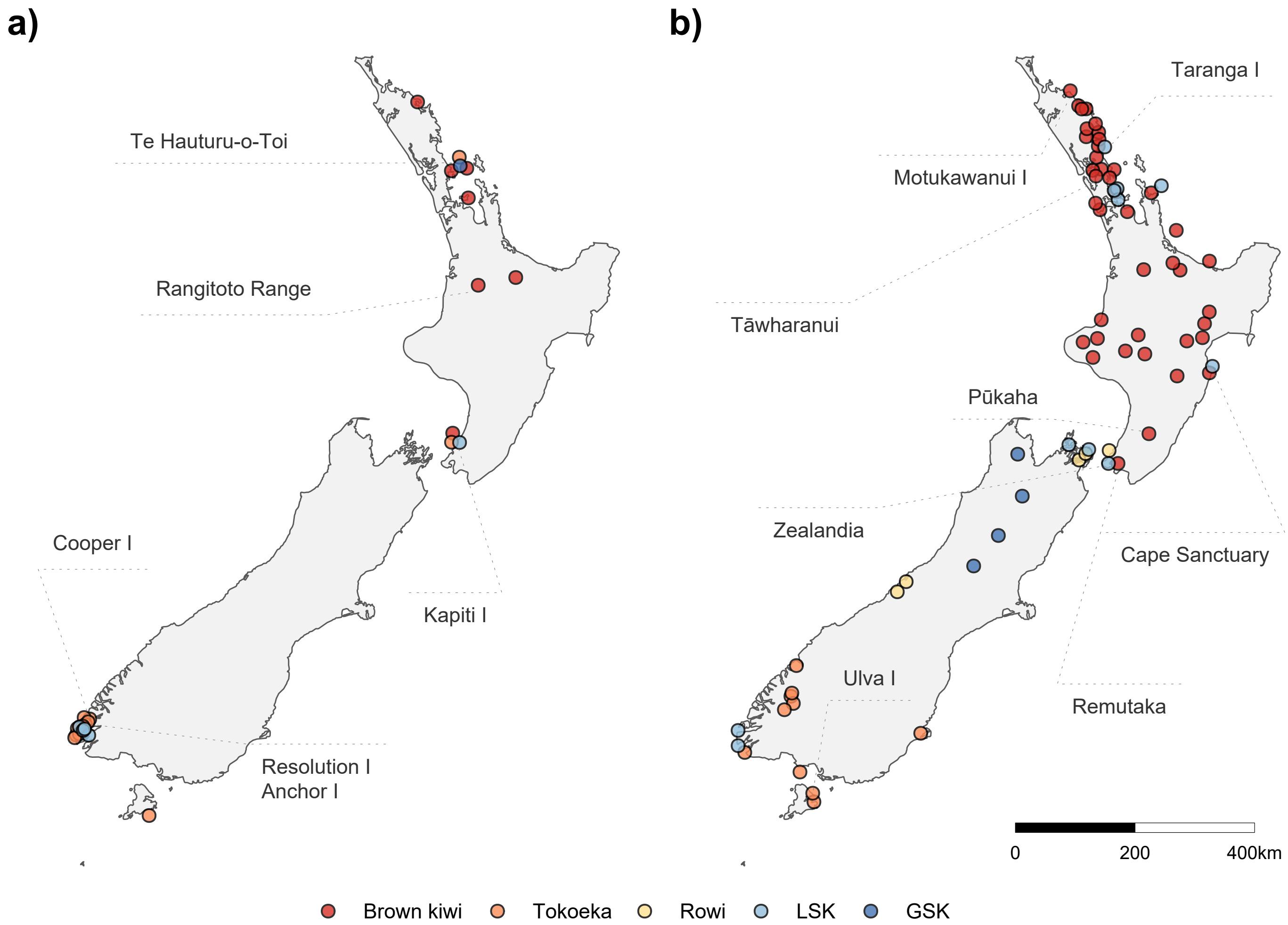

Figure 5. Sites of kiwi translocation projects for (a) historical (1863–1978) and (b) recent (1979–2018) periods. Each colour represents a different kiwi species: brown kiwi, tokoeka, rowi, little spotted kiwi (LSK), and great spotted kiwi (GSK). Translocations of LSK/rowi hybrids are grouped with translocations of rowi. Sites where more than one translocation project of the same species occurred, are shown only as one point. Sites where more than one species of kiwi were released (e.g. Kapiti Island, Te Hauturu-o-Toi/Little Barrier Island, or Cape Sanctuary) have points for each species displayed with a jitter factor of 0.01 arc degrees.

Conservation introductions of kiwi outside their historical range have been the dominant group of translocations. These introductions were mostly carried out either as assisted colonisations to islands, where kiwi were not previously recorded. In other cases, they were ecological replacements of extinct kiwi taxa, such as the introduction of brown kiwi to Pūkaha (2003) and the Remutakas (2006), a range previously occupied by extinct North Island rowi (Weir et al. 2016).

Reintroduction attempts first appear in the late 1970s/early 1980s in the Auckland region, with most of them occurring after 2000. Similarly, reinforcements of existing populations were mostly carried out after 2000, except for three early translocations to Resolution, Cooper, and Te Hauturu-o-Toi/ Little Barrier islands, as mentioned earlier. However, despite the recent increase of reintroductions and reinforcements, conservation introductions remained the largest group representing 40% of kiwi translocations in the last 20 years (1999–2018), followed by reinforcements and reintroductions with 35% and 25%, respectively.

Source of translocated birds

Before 1995, only wild-caught kiwi were translocated. With the introduction of the ONE programme in 1995 and releases of brown kiwi from captivity, the number of translocations relying only on wild-caught animals has declined markedly. Only 35% of translocations comprised exclusively of wild-caught animals in the last two decades. The share of translocation projects releasing exclusively ONE sourced birds in the same period increased to 25%, and only 5% (three minor reinforcement translocations) comprised birds solely from captivity. The remaining 35% of translocation projects consisted of a mix of birds sourced from a combination of wild, ONE, or captive populations. The shift towards ONE releases is most apparent for brown kiwi, rowi, and Haast tokoeka (translocations comprised exclusively of ONE birds) (Fig. 6). Translocations of little spotted kiwi, Fiordland tokoeka, and Rakiura tokoeka were all sourced solely from wild-caught birds. Great spotted kiwi translocations were predominantly sourced from wild-caught birds.

Habitat

Most kiwi translocation projects were to islands (55%), particularly during the early translocation period. There were no known cases of introductions or reintroductions to the mainland

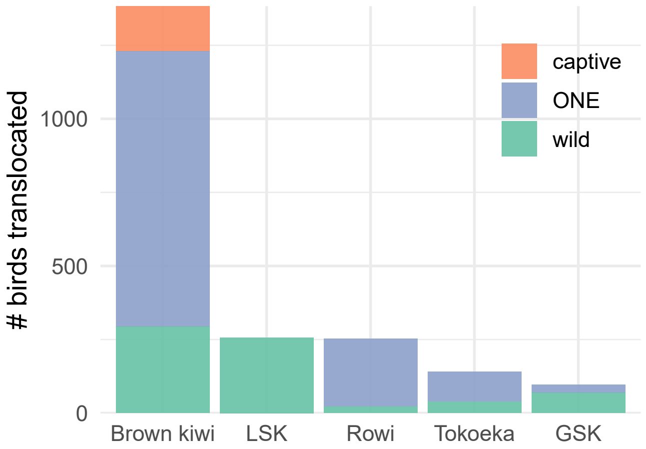

Figure 6. Numbers of translocated birds by source type between 1995–2018, following the introduction of the Operation Nest Egg (ONE) programme and releases from captivity. Most translocated brown kiwi, rowi, and tokoeka (Haast tokoeka) are sourced from the ONE programme. Before 1995, all translocated kiwi were wild-caught birds. Each bar represents a different kiwi species: brown kiwi, little spotted kiwi (LSK), rowi, tokoeka, and great spotted kiwi (GSK).

until the 1970s (Colbourne & Robertson 2000). Overall, 36% of translocations were to open mainland sites and the other 9% to ring- or peninsula-fenced sanctuaries. Translocations to the mainland became more frequent after 2000. Between 1999–2018, the share of translocations to islands dropped to 33%, while the share of translocations to mainland sites and fenced sanctuaries increased to 52% and 15%, respectively.

The median translocation project area was 800 ha (8–20 887, $n = 100$). Nevertheless, there were substantial differences in area among the translocation projects and, in several cases, the area size changed between individual releases for a single project. In the period 1979–2018, the median area of island projects was 218 ha (16–1509, $n = 31$), and fenced sanctuaries 450 ha (124–3363, $n = 9$), while mainland unfenced sites had a median area of 3000 ha (41–20 000, $n = 35$). Mainland sites substantially differed in size based on translocation type. Reintroduction and introduction project sites on the mainland had a median area of 1350 ha (41–19 000, $n = 19$), whereas reinforcement sites stretched over a median area of 3750 ha (210–20 000, $n = 16$).

Nearly half of all the release sites (49%) were considered free from the main predators targeting kiwi (stoat *Mustela erminea*, ferret *M. furo*, dog *Canis familiaris*, cat *Felis catus*) at the time of the releases, while 18% had one or more of these predators present and no predator control. These included sites with cats as the only main kiwi predator. The remaining 33% of sites had some level of sustained predator control management. The first translocation projects with ongoing predator control appeared only in the last two decades. Before 1999, 43% of translocations ($n = 42$) were to sites with no predator control (the last of these were in the 1980s), while 57% of translocations were to presumed predator-free sites, although anecdotal evidence suggests that some of them were invaded by predators soon after the kiwi releases (Colbourne 2005). Between 1999–2018, 43% of translocations ($n = 60$) were to predator-free sites, and 57% had some kind of predator control; 17% relied on trapping, 35% on a combination of trapping and poisoning (mostly by 1080/ sodium fluoroacetate), and 5% relied solely on aerial poisoning as a means of control.

Translocation objective

Historical records and the available literature indicate that early kiwi translocations were predominantly driven by emergency/ mitigation efforts and the establishment of secure populations due to expanding ranges of invasive predators, particularly around the turn of the 19th century. In the 1970s and 1980s, mitigation and emergency transfers were predominant due to the loss of habitat in Northland, mainly driven by logging of native forest. Translocations for meta-population and genetic management appeared in the 1980s for little spotted kiwi and have continued since. In the last three decades, the range of translocation objectives has diversified (Fig. 7). Ecosystem restoration and establishment of secure populations were typical objectives across all taxa while conservation advocacy appeared mainly among brown kiwi translocations. The rarest kiwi taxa, Haast tokoeka and rowi, were translocated chiefly to establish secure populations and to serve, eventually, as kōhanga/source sites.

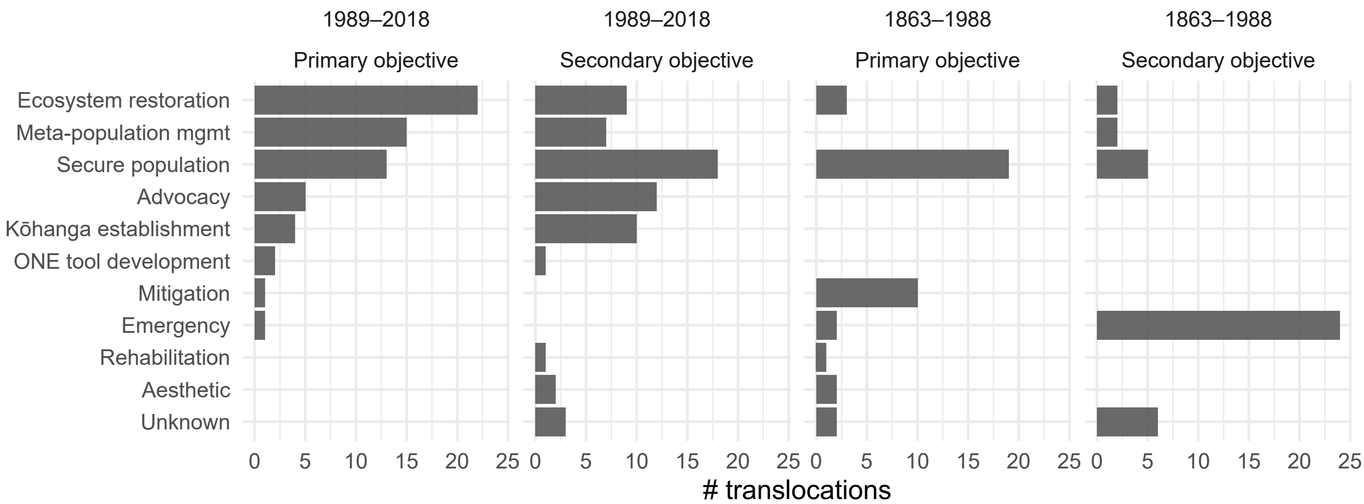

Figure 7. Primary and secondary objectives for all kiwi translocations between 1863–2018. The displayed split between the periods highlights the substantial shift of dominant objectives in the last three decades. Only overall translocation objectives were listed; some releases within a translocation project were carried out for multiple objectives.

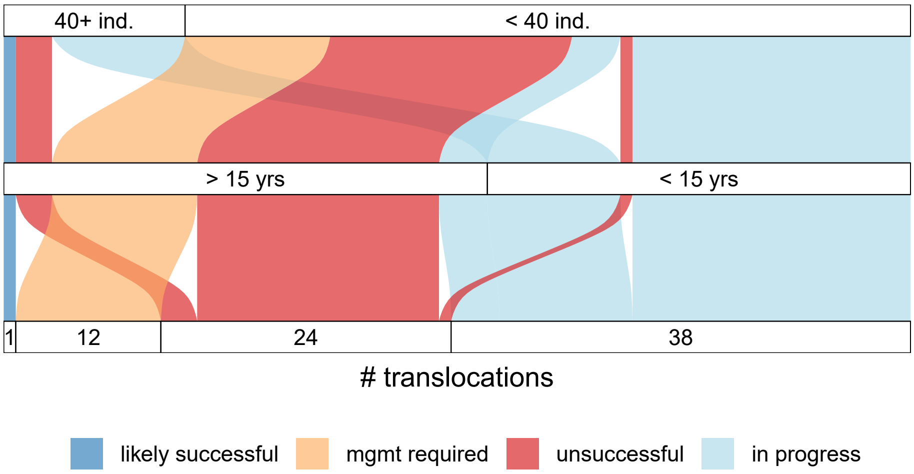

Figure 8. Outcomes of introductions and reintroductions ($n = 75$) between 1863–2018. Most recent kiwi introductions and reintroductions are still in progress, and most previous projects (before 2003) are either unsuccessful or require further management. Each colour represents an outcome category: likely successful, requiring further management, unsuccessful, and in progress. The top horizontal bar separates the translocations between projects releasing the recommended 40+ individuals and projects that have released less than 40 birds. The middle bar separates the translocations which were either finished or had released 40+ individuals more than 15 years ago (by 2003) and projects that are either ongoing or released 40+ individuals after 2003. The bottom bar shows the totals in each outcome category. Three introductions resulting in extant hybrid populations were not assessed, nor were 24 reinforcement translocations.

Translocation lead and reporting

Translocations have been initiated and led by multiple entities. The Department of Conservation (DOC) has played the dominant role in leading kiwi translocations since it was formed in 1987. In the last two decades, DOC or regional councils led 38% of translocation projects. In contrast, community groups and iwi/hapū led 25% and 3% of the projects, respectively. The remaining 33% were joint projects between DOC and either community groups or iwi/hapū. The information about earlier translocations is incomplete, but records suggest that pre-1987 translocations were also led by a variety of entities: The New Zealand Wildlife Service (a predecessor of DOC), community groups, reserve caretakers, and private initiatives.

Specific kiwi translocation projects are rarely reported in the scientific literature. Out of 76 translocations between 1979–2018, reports from only nine projects (12%) appear in scientific journals: four little spotted kiwi translocations (Jolly & Colbourne 1991; Colbourne & Robertson 1997), four brown kiwi projects (MacMillan 1990; McLennan & Potter 1992; Smuts-Kennedy & Parker 2013), and one great spotted kiwi project (Toy & Toy 2020). Information on a further 47 projects (62%) exists in reports, some published and publicly available, mainly through the DOC website, but most project reports remain solely as internal documents. For 20 projects (26%), reports either do not exist or were unavailable. Information about these projects is usually kept only as internal records. Recently, information about some projects has appeared on social media or in news reports. However, the focus of such information is mainly on release events, rather than long-term monitoring, or summarising lessons learnt.

Translocation outcome

We assessed translocation outcomes of 75 out of 102 translocations. The remaining 27 projects were not assessed as they were either reinforcements (24) or introductions resulting in hybrid populations (3). Out of the 75 assessed introductions or reintroductions, only 19 are known to have released at least 40 birds by 2018. However, only four projects had released at least 40 birds by 2003, so that at least 15 years had passed before the assessment date. Three of these failed and only one site, Zealandia, had a population increasing at a rate of more than 2% annually on average and therefore can be considered as a likely successful introduction/reintroduction as of 2018 (Fig. 8).

The sensitivity analysis categorising translocations revealed a similar pattern. Only 1–3 translocations were likely successful, based on different criteria values. When we reduced the assessment timeframe to ten years, three more sites received 40+ birds from 2004 to 2008. However, only one, Tāwharanui, could be considered likely successful due to its sustained population growth at this stage. When we increased the assessment timeframe to 20 years, no translocation would fit into the likely successful category. To identify translocations that were close to achieving a sufficiently genetically diverse founder population, we reduced the threshold number of released birds from 40 to 35. Only one project site received between 35–39 birds by 2003 and none in the period 2004–2008. Taranga (Hen) Island, received 38 birds and has shown a more than 2% average annual population increase so would fit into the likely successful category with these less restrictive criteria. When we increased the minimum number of released birds to 50, only two project sites, Resolution Island (LSK) and the Rangitoto Range, received 50+ birds by 2008. Nevertheless, both these introductions failed. Most assessed translocations (56 out of 75; 74.7%) released fewer than 40 individuals by 2018 and are therefore either classified as requiring further management, unsuccessful, or in progress. Here, we included eight projects where the number of transferred birds is not available or is uncertain, but is likely less than 40 individuals. We classified 12 established translocated populations with less than 40 released birds as requiring further management. Among these projects is little spotted kiwi on Kapiti Island, where it is unlikely that more birds will be added as there is no known wild population available for harvest. Also, most in progress projects (23 out of 38; 60.5%) released fewer than 40 birds by 2018. The remaining 15 in progress projects released 40+ birds after 2003, less than 15 years before our assessment was made. Previously translocated populations, which recently received additional birds by reinforcement, were also classified in progress, such as Motukawanui, Tiritiri Matangi, Red Mercury, and Ulva islands (Appendix S1 in Supplementary Materials).

Failed introduction or reintroduction projects, in which birds were subsequently removed, or where the population did not persist, were categorised as unsuccessful. In these instances, some individuals may still survive in the project area, but the population is considered functionally extinct. One third of the assessed translocations were unsuccessful projects (24 out of 75; 32%), but only three of these occurred in the last two decades. These recent unsuccessful attempts were projects where the translocated birds were removed following fatalities due to either starvation or predator incursion. The remaining 21 unsuccessful translocations were mostly early island releases from the late 19th/early 20th century or mitigation/emergency translocations from the 1970s and 1980s. Likely causes of failure in the first group were a combination of small founder populations, predator invasions, and insufficient habitat size (Colbourne 2005; Frankham et al. 2017). Failed translocations in the 1970s and 1980s to unfenced mainland sites suffered mainly from the lack of predator control, dispersal, and/or insufficient initial population size (MacMillan 1990; McLennan et al. 1996; Colbourne & Robertson 2000).

Monitoring of population establishment

A lack of detailed post-release monitoring data severely limited the evaluation of post-translocation survival and dispersal. No such data were collected, or data were unavailable, for kiwi translocations prior to 1979. Between 1979–2018, post-translocation monitoring information was available for 75% of all translocations (n = 76). Information from monitoring databases and survey reports was supplemented by reports on incidental deaths or sightings of released animals. Fewer projects had available information about survival longer than one-year post-release. Specifically, survival information was available for at least a subset of released birds for one full year (70% of projects), three years (46%), and five years (30%) post-release.

In the last two decades (1999–2018), radio-telemetry was the primary type of post-release monitoring (72% of all projects, n = 60). Call counts and other acoustic monitoring were the second most common (13%), followed by recapture surveys (8%). Information for the remaining 7% of the projects was unavailable, or no monitoring was carried out. Many projects, particularly the longer running ones, used various types of monitoring methods at different stages of the project or for different releases. In many cases, radio-telemetry was replaced with acoustic recorders or call count surveys. Infrequent recapture surveys with trained dogs or playback calls tended to be used mostly on islands where other types of monitoring were deemed impractical.

Post-release effects – mortality and dispersal

Post-translocation survival in the release area was affected by a combination of mortality and dispersal of released birds. Between 1999–2018, 47 out of 60 (78.3%) translocation projects collected some information about post-release survival and mortality, including its causes (Table 1). Out of the 47 projects, 72% recorded dead birds among successfully released individuals (for all but one project, these deaths were within three years post-release). Despite the effort by managers to identify the causes of death, 45% of projects with survival/mortality information (n = 47) reported kiwi mortality of unknown or uncertain causes. Misadventure, as a cause of death, particularly by drowning and falls, was recorded at 40% of the projects. Although misadventure and unknown causes of death appeared at all site types, rates of predation varied widely between unfenced mainland sites on the one hand, and islands and fenced sanctuaries on the other. Sixty-five per cent of mainland projects (15 out of 23 projects with information on mortality) recorded predation of released kiwi. The birds

Table 1. Reported causes of kiwi mortality in translocation projects between 1999–2018. The table shows the numbers of projects where different causes of mortality occurred irrespective of their frequency, monitoring length, or effort. Predation was reported as the main cause of death at unfenced mainland sites despite predator control measures. We included reported incidents up to 12 years post-release to capture rare events, such as ferret or dog predation, affecting the long-term outcome of translocations. Misadventure includes injuries, falls, and drownings.

Reported cause of mortality	mainland	fenced	island	all sites
predation all	**15**	**1**		**16**
by mustelids (stoat, ferret, weasel)	**13**	**1**		**14**
by ferret	**7**			**7**
by dog	**7**			**7**
by cat	**1**			**1**
car strike	3			**3**
misadventure	10	5	4	**19**
malnutrition	3	1	3	**7**
disease	2	4	1	**7**
transmitter entanglement	1	1	2	**4**
unknown	13	3	5	**21**
no mortality	4	1	8	**13**
projects with information	**23**	**8**	**16**	**47**
projects without information	8	1	4	13
all projects	31	9	20	60

were mainly depredated by mustelids – predominantly stoats, but also ferrets, which were confirmed at 30% (7) of mainland sites. Predation by dogs was also an issue at 30% (7) of sites.

In contrast, no island translocations reported predation of released kiwi between 1999–2018. However, stoat incursions occur repeatedly on islands near the mainland, such as in the case of Pomona Island at Lake Manapouri. In one case in 1982, previously released little spotted kiwi were removed from Maud Island to avert predation by newly-invading stoats (Colbourne 2005). The situation was similar at fenced sanctuaries. Only one fenced sanctuary, which did not eradicate stoats, reported stoat predation. Two other fenced sanctuaries reported rare stoat incursions but no associated kiwi mortality.

Dispersal of released birds beyond the project area was a significant issue influencing population establishment, particularly at the unfenced mainland sites. There were no reports of kiwi dispersing from islands, and there was only one known report of a kiwi dispersing from a peninsula-fenced sanctuary, likely through a gap between the beach end of the fence and the waterline. Dispersal from protected project areas appears to be a frequent issue at unfenced mainland sites. Between 1999–2018, 64% of unfenced mainland projects (n = 22) with available information reported dispersal of at least some individuals to outside the project area within the first-year post-release. Sites with an area less than 3000 ha (median area of mainland sites) had one dispersed bird per three known surviving birds by the end of the first-year post-release. In contrast, sites of 3000+ ha had one dispersed bird per 24 known surviving birds. At most mainland projects with reported post-release dispersal (at least eight out of 11), some or all wandering kiwi were brought back to the project area by managers. Several of the dispersing birds were brought back repeatedly.

Survival Model

The model estimating survival time of translocated kiwi showed considerable uncertainty in the model estimates due to the lack of precision in survival information and the small sample size within categories. Nevertheless, there were some clear patterns in the data (Fig. 9), such as evidence (posterior probability 0.92) for longer survival of birds released into predator-free sites compared to large sites (3000+ ha) with sustained predator control. We also found evidence for longer survival times of birds in predator-free sites compared to small sites (< 3000 ha) with predator control and unmanaged sites (both posterior probabilities > 0.99). Note, however, that the survival data from unmanaged sites came entirely from earlier translocations of only wild birds with no releases of ONE or captive birds. We found substantial evidence (posterior probability 0.82) for longer mean survival times in large sites than small sites with ongoing predator control.

Additionally, the post-release survival of wild and captive birds was higher than that of ONE birds (both posterior probabilities > 0.99) but there was no difference between captive and wild-caught birds. The expected annual survival rates of the released birds are shown in Table 2. There was no difference in mean survival times of birds released as part of reinforcement translocations compared to introductions and reintroductions. Similarly, there were no substantial differences among the mean survival times of various kiwi taxa. Nevertheless, we found substantial differences among individual translocation projects, which indicate the existence of unmeasured factors at the project level that may explain variances in estimated mean survival time. These factors may include the quality and

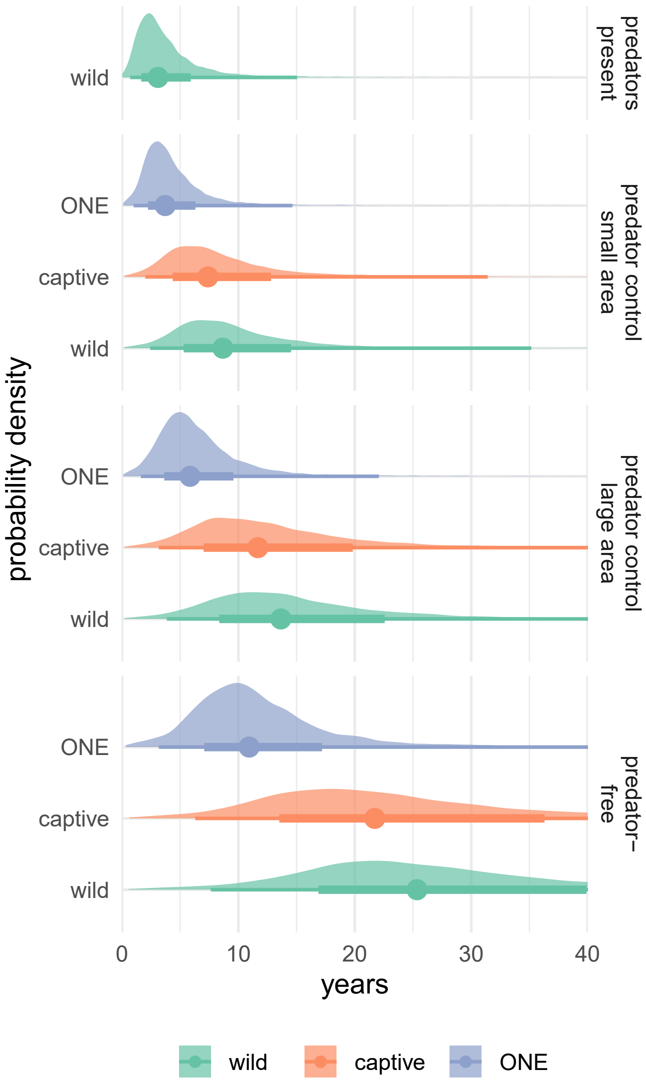

Figure 9. Density distributions of the expected mean survival times of translocated birds for different types of predator status of the project area. The dot represents the median and error bars display 66% and 95% credible intervals. Predator-free sites where wild-caught or captive birds were released exhibit the longest expected survival times, whereas sites where predators were present and uncontrolled show the shortest survival times. The defining line between small and large areas with predator control was size 3000 ha – the median area of mainland unfenced sites. Different colours represent different bird source types: wild-caught birds, captive facilities, and birds from the Operation Nest Egg (ONE) programme. Only wild-caught birds are shown for unmanaged sites with predators present as there were no recorded releases of captive or ONE birds to such sites.

Table 2. Expected annual survival rates (%) and expected median survival times for different source types of translocated birds – wild-caught birds, captive facilities, birds from the Operation Nest Egg (ONE) programme – and different types of predator status of the project area (see Fig. 9 for more detail). Values represent a median survival rate (%) with 95% credible intervals in brackets assuming constant hazard over time. A value of zero was assigned when it was not possible to calculate the annual survival rate due to an expected survival time of < 1 year.

Source type	predator-free	predator control large area	predator control small area	predators present
wild	96 (87–99) *25.3 years*	93 (74–98) *13.6 years*	88 (59–97) *8.7 years*	68 (0–93) *3.1 years*
captive	95 (84–99) *21.7 years*	91 (68–98) *11.7 years*	86 (50–97) *7.4 years*	—
ONE	91 (68–98) *10.9 years*	83 (39–95) *5.8 years*	73 (1–93) *3.7 years*	—

type of predator control, the abundance and suite of predators in the project area and the surrounding landscape, the age of released birds, or other factors not included in our model.

Breeding of the released birds

Information on breeding by released birds within the dataset was scarce. Between 1999–2018, only 33% of all translocation projects ($n = 60$) reported breeding of the released birds within five years post-release. This information is mostly limited to signs of breeding attempts or successful hatching of chicks, and information about offspring recruitment into the breeding population is usually unavailable. During the first-year post-release, 75% of the projects (15 out of 20) reported breeding attempts among some of the released birds. This rose to 95% of the projects (19 out of 20) reporting breeding birds within three years post-release, which was mostly attributed to ONE birds reaching sexual maturity. During the first-year post-release, only 6% of reported breeders ($n = 112$) were ONE birds, while the share of wild and captive birds was 79% and 15%, respectively.

Discussion

We reviewed kiwi translocations since the 19th century, summarised information on translocated birds and translocation projects and evaluated their outcomes. Even though only a small number of translocations can be considered likely successful in establishing a self-sustaining population as of 2018, and for many translocations it is too early to make an assessment, we identified factors affecting the survival of released birds, which contribute to the translocation outcome.

The dataset of kiwi translocation projects we reviewed is more extensive than in previously published reviews and summaries (Atkinson 1990; McHalick 1998; Colbourne & Robertson 2000; Colbourne 2005; Cromarty & Alderson 2013; Miskelly & Powlesland 2013; Seddon et al. 2015). We are confident that the dataset contains an overwhelming majority of all kiwi translocation projects. There were uncertainties about several historical translocations, particularly to Kawau, Kapiti, Horomamae/Owen, and Motukiekie islands (Jolly & Daugherty 2002; Colbourne & Robertson 2004; Colbourne 2005), but despite the lack of or conflicting information about the exact year of releases or numbers of translocated birds, they appeared sufficiently credible to be included.

We encountered uncertainties about the historical ranges of kiwi taxa and the presence or absence of conspecifics at the time of the release, which affected the categorisation of projects as introduction (including assisted colonisation and ecological replacement), reintroduction, and reinforcement (Seddon 2010). Managers often classified kiwi translocations as reintroductions, but we re-interpreted some as assisted colonisations or ecological replacements of previously extinct taxa, based on former distributions of kiwi (Shepherd et al. 2012; Weir et al. 2016; Germano et al. 2018). We assumed that most kiwi translocations to islands were introductions, similar to Seddon et al. (2015), although kiwi naturally occurred on several large islands in the proximity of the mainland, such as D'Urville (Jolly & Daugherty 2002), Secretary, Resolution, and presumably Cooper Island (Henry 1895; Colbourne 2005) or Te Hauturu-o-Toi/Little Barrier Island (Palma 1991). Hence, historical translocations of tokoeka to Resolution, little spotted kiwi to Cooper Island, and brown kiwi to Te Hauturu-o-Toi were considered reinforcements.

Translocation effort and conservation status

Over the last four decades, birds from the North Island taxa (brown and little spotted kiwi) were disproportionately more frequently translocated compared to the South and Stewart Island taxa with large overall population sizes. Only the rarest taxa from the South Island, rowi and Haast tokoeka, had markedly higher proportions of translocated birds compared to their populations due to intensive conservation management and small population size (Fig. 4). A similar pattern in general kiwi management was identified by Innes et al. (2015b). In their assessment, great spotted kiwi, Fiordland and Rakiura tokoeka receive the least conservation management, and their overall populations are declining. In contrast, the North Island taxa, rowi, and Haast tokoeka have higher proportions of the population under some management regime and are generally increasing.

The kiwi taxa that receive relatively little management, including only a few or no translocations, have moved to more threatened conservation status in recent years, whereas those with more management, including more translocations, generally improved their conservation status. Brown kiwi is no longer considered threatened as its status improved between 2012–2016 to at risk/declining (Robertson et al. 2017). Similarly, little spotted kiwi, which has been repeatedly listed nationally as at risk/recovering, improved its conservation status on the IUCN Red List from vulnerable to near threatened category between 2004–2008 (BirdLife International 2016). The status of rowi improved from nationally critical to nationally vulnerable between 2012–2016, whereas Haast tokoeka remained nationally critical due to very low numbers and ongoing recruitment failure. In contrast, the status of great spotted kiwi and North Fiordland tokoeka worsened from gradual decline in 2005 to nationally vulnerable in 2008 and have remained at that level (Hitchmough et al. 2007; Miskelly et al. 2008; Robertson et al. 2017). Rakiura and South Fiordland tokoeka were considered nationally vulnerable, but both were reclassified as nationally endangered between 2008–2016 (Robertson et al. 2013; Robertson et al. 2017).

Even though a higher translocation effort may indicate an improvement in the conservation status of kiwi taxa, it is likely related to their respective population sizes. For example, the rare kiwi taxa would not survive or be recovering without translocations (Seddon et al. 2015). Little spotted kiwi currently persist only in translocated populations and the major range expansions of little spotted kiwi, Haast tokoeka, and rowi can be attributed solely to management by translocations. In contrast, the population increase of brown kiwi taxa is mainly attributed to improved and expanded in situ management through predator control, while translocations played only a minor role in the species' recovery (Innes et al. 2015b). Similarly, the most populous South and Stewart Island kiwi taxa do not appear to be declining because of the low translocation effort, but because of the lack of landscape-scale predator control across most of their current range (Innes et al. 2016). Therefore, the use of translocations in reversing population decline and improving conservation status appears to have a substantial impact only in the rarest kiwi taxa: Haast tokoeka, rowi, and little spotted kiwi.

Translocation objectives

Establishing secure populations was a common translocation objective for most kiwi taxa over the last two decades. Similarly, translocations carried out as part of meta-population management or for establishing kōhanga/source populations for future translocations were relatively common in little spotted kiwi, rowi, and Haast tokoeka – the three most management-dependent taxa with the smallest populations. Given the improving conservation status of brown kiwi and little spotted kiwi, these taxa have been translocated in the last 20 years for a wider set of objectives, such as ecosystem restoration and conservation advocacy (Innes et al. 2015a; Nally & Adams 2015). These translocations have not been driven primarily by species-oriented conservation but instead by attempts to restore native ecological communities through pest eradication or suppression, alongside reintroductions of a broad suite of native species (Saunders & Norton 2001; Miskelly 2009). In some instances, advocacy and public engagement were the main objectives for translocations, which may create a possible conflict of interest between species recovery and public demand (Nally & Adams 2015).

The outcome of reintroductions and conservation introductions

Improving outcomes of translocations is an important element of kiwi recovery management (Germano et al. 2018) as well as of continued public support for this conservation tool (Jachowski et al. 2016). The number of populations initiated through translocations is increasing, which contributes to one of the main kiwi recovery goals: restoring former distributions of all kiwi taxa. Translocations also expand beyond the former distributions, by creating new populations on islands, or through ecological replacements of kiwi taxa that are now extinct. However, it is not immediately evident if these newly established populations will grow and maintain sufficient genetic diversity, and therefore if they contribute to the other two kiwi recovery goals (growing populations of all taxa and maintaining their genetic diversity), which are crucial for population persistence (Converse & Armstrong 2016; Nelson et al. 2019).

Kiwi translocations have been reported as successful in internal transfer reports and scientific literature, usually based only on initial survival of released birds and/or signs of breeding (Colbourne & Robertson 1997; Miskelly & Powlesland 2013; Smuts-Kennedy & Parker 2013) unless there was an apparent failure of kiwi to establish at the release area (MacMillan 1990; McLennan & Potter 1992). However, this perceived success does not necessarily lead to a self-sustaining population (Wolf et al. 1998; Brichieri-Colombi & Moehrenschlager 2016). Also, those assessments generally did not consider the genetic make-up of newly-established populations and the consequences of small founder numbers, which have been highlighted only in the last two decades (Briskie & Mackintosh 2004; Groombridge et al. 2012; Jamieson & Lacy 2012; Taylor et al. 2017).

Based on our categorisation, kiwi translocations appear to have a lower-than-expected success rate. Only one out of 75 introductions and reintroductions can be considered likely successful at the 15-year mark with the caveat that this population was, unavoidably, sourced from a previously severely bottlenecked population, which may have negative implications in the future (Ramstad et al. 2013). The number of likely successful translocations increases to two if we reduce the in progress period from 15 to 10 years, and three if we also reduce the required number of released birds from 40 to 35. In contrast, one third of all assessed projects (24) were unsuccessful. However, nearly half of these projects failed more than 100 years ago and only three failed in the last two decades. Half of all assessed projects (38) were still in progress, and we categorised the remaining 12 translocations as requiring further management. All translocations in this group were previously considered successful due to achievement of population establishment and growth (Colbourne & Robertson 1997; Miskelly & Powlesland 2013). However, several of these populations were established with a small number of individuals (5–38, two projects unknown), and it has become apparent that they may suffer from inbreeding depression despite successful establishment and initially strong population growth (Taylor et al. 2017). Several of these populations have been recently supplemented by reinforcement translocations to improve their genetic diversity (Robertson et al. 2019b, 2019c) and therefore, we considered them as projects in progress. These meta-population management efforts appear to be an exception for rare (little spotted kiwi) or endangered taxa (Rakiura tokoeka). The need for meta-population management in little spotted kiwi is amplified by the fact that the entire known population of the species likely descends only from a few birds translocated to Kapiti Island more than a century ago and most recent populations were established with less than 40 individuals (Taylor et al. 2017). Most management plans for other kiwi taxa do not explicitly address the issue of the genetic health of previously established populations with low founder numbers.

Nearly half of all kiwi translocations (50) commenced, and 76% of all translocated birds were released after 2003.

Thirty-eight per cent of these projects were reinforcements, which were not assessed similarly to introductions and reintroductions. Reinforcements were carried out for a large variety of objectives, from mitigation/emergency transfers to meta-population management, and the numbers of released birds varied widely (1–100+) and are not directly comparable between each other (Fischer & Lindenmayer 2000). Fifty-eight per cent of the translocations started after 2003 were introductions and reintroductions that we categorised as in progress; only one project has definitely failed, because of ferret predation. Several other introductions and reintroductions that are in progress suffer from population declines due to high mortality and dispersal and/or lack clear plans to release the recommended 40 individuals for a genetically diverse and self-sustainable population; these projects are on a trajectory towards the requiring further management or unsuccessful categories after the 15-year benchmark we used for assessment. In contrast, some translocations with higher numbers of released birds to pest-free sites or larger sites with intensive predator control already show signs of positive population growth, the essential precursor to long-term translocation success (Armstrong & Reynolds 2012).

Population establishment

An overall translocation outcome depends on multiple factors, but a prerequisite of a successful translocation project is the establishment of the population at the release area. Despite identifying only one translocation, or possibly up to three, that are considered likely successful at the time of our assessment, we attempted to determine factors that contribute to translocation success in the future across all translocation types. In particular, we focused on the post-release effects and factors affecting post-translocation survival at the release site, which determine the prospects of population establishment (Tavecchia et al. 2009).

Survival modelling clearly shows differences in mean survival time of translocated birds based on the source type of released birds as well as predator status at the release site, despite wide credible intervals caused by the lack of long-term monitoring data. Information on the exact time of death or dispersal for more of the released kiwi would have allowed more robust predictions. Wild-caught birds and birds from captivity appear to survive for much longer than birds from the ONE programme. Kiwi from captive facilities showed similar mean survival times to wild birds, which is surprising in light of reviews identifying translocations of captive animals as less successful for many species (Griffith et al. 1989; Fischer & Lindenmayer 2000). However, other studies (Miskelly & Powlesland 2013; Brichieri-Colombi & Moehrenschlager 2016) showed that releases of wild and captive animals have similar outcomes. Lower median survival rates of translocated ONE birds were consistent with lower survival rates of ONE subadults and juveniles released back to their source populations, compared to survival rates of wild adults of various kiwi taxa in those populations (Robertson et al. 2011; Robertson & de Monchy 2012). However, in those populations the wild adults were resident birds with established territories and therefore the situation is not directly comparable to translocations of both wild and ONE birds into unoccupied areas. The shorter mean survival time of ONE birds was likely caused by higher rates of mortality related to misadventure, but also a higher susceptibility to predation due to the young age of most ONE birds at the time of their release (McLennan et al. 1996; Robertson et al. 2011).

Mean survival times for birds released to predator-free environments were substantially higher than to areas with ongoing predator control and large areas performed better than smaller project sites. Predator-free sites were generally islands (Colbourne 2005; Bellingham et al. 2010) or fenced sanctuaries, where the main predators of kiwi were eradicated and where necessary measures against reinvasion have been in place (Burns et al. 2012; Innes et al. 2015a). Sites with ongoing or no predator control were mainly unfenced mainland sites with a range of kiwi predators at varying densities. Two-thirds of the project sites with ongoing predator control still reported issues with predation of the released birds, mostly by mustelids. Given many unknown causes of mortality, the real proportion of mainland translocation projects affected by predation is likely to be higher. The list of reported predators is similar to other studies on kiwi survival (McLennan et al. 1996; Basse et al. 1999; Innes et al. 2010).

Post-translocation dispersal is very likely to be another major factor affecting population establishment at unfenced mainland sites, as has been found in other studies (Brichieri-Colombi & Moehrenschlager 2016; Berger-Tal et al. 2019). While predator-free sites benefited from natural or artificial barriers limiting incursions of predators, these barriers also prevented kiwi from dispersing outside the project areas. Both the reduced risk of predation and reduced dispersal out of predator-free sites likely contributed to markedly higher survival times than at unfenced mainland sites. Smaller unfenced mainland areas were presumably more affected by dispersal than large sites, which allowed post-release dispersal of more birds to occur within the limits of the project areas.

Genetic considerations

The current official guidance for kiwi introductions and reintroductions is to release 40 individuals to establish a founding population (Sporle 2013; Robertson & Colbourne 2017). This recommendation is based on the modelling of retention of rare alleles for brown kiwi and estimates of the founder numbers required to preserve the genetic diversity essential for population viability (Weiser et al. 2013; Weiser 2014) and maintenance of its adaptive potential (Weeks et al. 2015). However, there are several other requirements that need to be met to maintain the desired level of genetic diversity, including 90% post-release survival, no dispersal, a high proportion of breeders among released individuals (> 90%), a predator-free environment, and a sufficient carrying capacity of the project area to allow for population growth. Furthermore, given the lower survival rates of translocated juvenile and subadult kiwi, more young birds should be released to retain the same level of allelic diversity within a new population than within a population established by releasing adults alone (Weiser 2014).

The reality of translocation often diverges from these requirements. At three predator-free sites, where populations were established by wild-caught and mainly adult little spotted kiwi, the estimated proportion of effective founders (released birds that successfully produced offspring) within the total numbers of translocated birds was highly variable (40–81%). Such low proportions of successful breeders suggest a significant loss of the source population's genetic diversity within the new populations (Ramstad et al. 2013), which is likely common among translocations of other kiwi taxa as well. Similarly, given the lower mean survival times at sites with predator control and where populations were established by ONE birds, we could infer that the number of released birds needs to be much higher than the suggested 40 birds to maintain the desired level of genetic diversity.

Recommendations

Advances in translocation practice, such as implementing a regulatory framework (Nally & Adams 2015) and providing official guidance (Robertson & Colbourne 2017), have helped to increase prospects of recent translocations. Still, the increasing popularity of kiwi translocations brings challenges relating not only to the sufficient size of founder populations but also in the continuation of habitat management, which is critical for the achievement of long-term recovery objectives (Grant et al. 2019). A successful translocation has been traditionally understood to be the establishment of a self-sustaining population (Griffith et al. 1989; Fischer & Lindenmayer 2000). However, long-term habitat management in terms of predator control (Stadtmann & Seddon 2020) and management of genetic diversity may be necessary for long-term persistence (Hayward & Slotow 2016). Cryptic inbreeding depression in isolated bottlenecked populations or ongoing predator incursions may pose significant threats to the persistence of translocated populations. Therefore, continued monitoring of translocated populations and adaptive management are crucial.

From the available data, it is apparent that each introduction/reintroduction project needs to plan for a specific number of released birds based on a combination of factors, such as predator status of the project area, its size, the age structure and source(s) of released birds, and dispersal probability. Managers need to account for the loss of genetic diversity caused by the differences in survival rates, causes of mortality, or the carrying capacity, and the boundary type of the project area (Department of Conservation 2018). Left unchecked, the genetic consequences of small founder size of translocated populations have the potential to reduce the fitness of birds, increase rates of hatching failure, and decrease the overall population viability (Briskie & Mackintosh 2004; Heber & Briskie 2010; Frankham et al. 2017). Such reduced viability of a newly established population has already been observed in little spotted kiwi on Long Island (Taylor et al. 2017), but it is likely more widespread (Ramstad et al. 2013). This issue underscores the importance of genetic monitoring and management to address the risk of genetic drift and inbreeding depression in translocated populations (Weeks et al. 2015; Biebach et al. 2016; Frankham et al. 2019). Long-term genetic monitoring will also enable assessment of the effectiveness of reinforcements, to identify whether the translocated birds successfully contribute to the gene pool of the resident wild population (Fischer & Lindenmayer 2000).

At mainland unfenced sites, sufficient space for post-release dispersal or natural dispersal of future juveniles and subadults needs to be available to reduce losses of released birds and their offspring. If no additional habitat is available to enlarge the project area, managers may need to follow up with periodic releases to compensate for the loss of dispersed individuals and facilitate necessary gene flow between populations (Brown et al. 2015; Richardson et al. 2015; Gitzen et al. 2016). Nearly all of the mainland unfenced sites where kiwi were established in the last two decades were smaller than the recommended 10 000 ha. Smaller areas may not provide sufficient habitat for natural juvenile dispersal and compromise population viability due to higher rates of emigration and predator incursions (Basse & McLennan 2003; Westbrooke 2007; Brown et al. 2015). Between 1999–2018, more than half of the unfenced mainland projects established a population at an area smaller than 1500 ha, which resulted in substantial rates of dispersal outside the project area. However, even when kiwi were released to larger areas, there were instances of release burrows being located near the boundaries of the project area, which diminished the buffer zone effect for dispersal. Currently proposed translocation guidelines recommend a project area size with a carrying capacity of at least 100 pairs to accommodate population growth and enable maintenance of genetic diversity. This approach acknowledges variability in kiwi densities for different taxa and different habitats (Department of Conservation 2018), but the habitat availability for post-release and juvenile dispersal needs to be considered as well.

Similarly, habitat quality, including predator status, is a crucial factor for the outcome of translocations (Sheean et al. 2012; Brichieri-Colombi & Moehrenschlager 2016; Stadtmann & Seddon 2020). Small, unfenced areas may not provide sufficient habitat quality for population persistence even with intensive predator management (Brown et al. 2015). Extensive buffer zones with predator control around unfenced project sites may reduce predator incursions and associated kiwi mortality. Notably, control measures for wide-ranging ferrets in the areas surrounding project sites may be necessary to reduce deaths within translocated populations. Long-term habitat suitability and the propensity for stochastic events should also be considered when selecting sites for kiwi translocations. Instances of droughts on Tiritiri Matangi and Red Mercury islands, leading to kiwi mortality and the reduction of carrying capacity (Robertson et al. 2019b, 2019c), demonstrate the need for careful assessment of long-term viability of such kiwi populations at isolated sites with changeable habitat quality.

Translocated populations must be adequately monitored, and the translocation outcomes reported. Post-release effects play an important role in population establishment and should be addressed by managers to reduce mortality and dispersal, particularly of ONE birds. Appropriate release strategies, such as releasing ONE birds in larger groups and outside of winter and autumn months, may significantly increase survival, as demonstrated in rowi (Batson et al. 2015). However, the most suitable season for release may differ among kiwi taxa (Robertson & Colbourne 2017). Modelling of survival times suggests that releases of ONE birds are best suited for predator-free sites to maximise chances of these birds to settle, mature, and breed successfully. Sufficiently long and standardised post-release monitoring (Sutherland et al. 2010) will facilitate addressing possible issues, inform subsequent adaptive management, and allow for planning of additional releases, if needed, to supplement the founder population (McCarthy et al. 2012). Reporting of demographic data from monitoring, together with details on habitat variables and applied management tools, is essential to further increase the effectiveness of future translocations (Moro et al. 2015; Gitzen et al. 2016).

Conclusions

We reviewed 102 kiwi translocations from the 19th century until the present to assist with the refinement of the translocation process and guidelines (Batson et al. 2015), and to inform the upcoming kiwi translocation strategy (Germano et al. 2018). Translocations of kiwi have grown in the last two decades, both in numbers of translocated birds and the number of new translocation projects. There has been a marked increase of projects focusing on ecosystem restoration by releasing less threatened taxa of kiwi in the proximity of urban areas and a shift from the government towards community groups undertaking the translocations (Nally & Adams 2015). During the same period, establishment and reinforcement of kiwi populations on the mainland became the dominant type of kiwi translocations, and releases to fenced sanctuaries were pioneered. However, releases to predator-free islands increased as well, mainly in the last ten years.

Because kiwi are long-lived, most recent kiwi translocations are considered as in progress. However, our analysis shows that despite their growing popularity, and improvement in their planning and management, kiwi translocations face similar issues as translocation projects of other species worldwide (Berger-Tal et al. 2019). Unfenced mainland project sites suffer from predation, which highlights the common overestimation of the efficacy of predator control measures and overall habitat suitability in translocation proposals, particularly at smaller sites, which are affected the most. An overestimation of habitat suitability also occurs at predator-free sites. Notably, islands may suffer from droughts causing a reduction in habitat carrying capacity and increased risk of translocation failure due to small population size (Robert et al. 2015). Behavioural issues, such as post-release dispersal and learning incidents, exacerbate adverse post-release effects, particularly at unfenced mainland sites and in releases of subadult and juvenile ONE birds. Such issues cause substantial differences in mean survival times and thus differences in the probability of translocation failure among various projects, based on the source type of the released birds, predator status, and size of the project area.

In our framework for the evaluation of introduction/reintroduction outcomes, we focused on the recommended number of released birds as one of the metrics for likely translocation success. Current guidance is to release 40 unrelated starters to become the founders of a new population (Robertson & Colbourne 2017). However, differences in expected survival times and time until breeding occurs revealed the need for project-specific adjustments of the number of released birds to achieve similar targets for the retention of genetic diversity. For projects where higher rates of mortality, dispersal, and delayed breeding is expected, substantially more released birds will be required. Consequently, past or recent translocations with lower numbers of effective founders will likely need further releases or periodic meta-population transfers to achieve genetically robust and thriving populations (Weeks et al. 2011) that contribute to the kiwi recovery goals.

Adaptive management based on appropriate demographic and genetic monitoring will facilitate the long-term persistence of the translocated populations. Information stemming from such management and monitoring will further inform best practice for kiwi translocations and broader applications of reintroduction biology.

Acknowledgements

We are thankful to all data providers and people who collected the data in the field: members of community groups, tangata whenua, and staff of the Department of Conservation. We also thank the Kiwi Recovery Group members, particularly Jess Scrimgeour, Hugh Robertson, Rogan Colbourne, and Isabel Castro, for their input and feedback, and to Kiwis for Kiwi and the Zoo and Aquarium Association for the assistance with obtaining and interpreting the data. We are thankful to two anonymous reviewers for their insightful comments to improve the manuscript. PJ was supported by a Lincoln University Doctoral Scholarship.

Author contributions

PJ, LM, JR, and JG all contributed to the conceptualising of the study; PJ and FC designed the methodology and undertook the data analysis. PJ wrote the manuscript and all other authors reviewed and contributed text. Data curation and visualisation were undertaken by PJ.

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Received: 28 October 2020; accepted: 7 June 2021
Editorial board member: George Perry

Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. List of translocations projects.

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