Improved methods for reducing translocation mortality and obtaining reliable population projections for reintroduction of the New Zealand Rifleman *Acanthisitta chloris*

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Summary

Despite many notable successes, the failure rate of animal translocations remains high. Conservation practitioners and reintroduction specialists have emphasised the need for ongoing documentation of translocation attempts, whether successful or not, including detailed methodologies and monitoring approaches. This study reports on the first translocation of the North Island subspecies of New Zealand's smallest bird, the endemic Rifleman Acanthisitta chloris granti. We describe an improved transfer methodology following recommendations arising from a previous translocation of South Island Rifleman Acanthisitta chloris chloris. Key modifications included a reduced capture window, shorter holding times, lack of extended aviary housing, and separation of territorial individuals during holding. Survival from capture to release increased from 52% to 97% using this new methodology. However, only 22% of 83 released birds were found in the reserve the next breeding season, resulting in an initial breeding population of only six males and five females. An integrated Bayesian analysis of three years of subsequent population data, including a population boost from a second translocation, projected a median decrease to 0–5 females over 10 years, but with 95% prediction intervals ranging from 0 to 33. These projections explicitly account for parameter uncertainty, as well as demographic stochasticity, and illustrate the need to do so when making inferences for small reintroduced populations.

Introduction

Conservation programmes and restoration plans often map out strategies that include the reintroduction of locally extinct species via translocation (Parker 2008). Conservation translocations are a vital tool for management of both endangered species and of recovering ecosystems because re-establishment of populations of threatened species enhances biodiversity and therefore helps to maintain broader level ecosystem functions and processes (Schlapfer and Schmid 1999, Benayas *et al.* 2009). Translocation now has a proven track record as an effective tool for both the management of individual species and the restoration of ecosystems (Armstrong and McLean 1995, Parker 2008, Seddon *et al.* 2014). Despite the many successes, a high proportion of translocations fail to establish viable populations or reach the population size goals set by managers at the outset (Griffith *et al.* 1989, Wolf *et al.* 1998, Fischer and Lindenmayer 2000, Oro *et al.* 2011, Ebrahimi *et al.* 2015).

Whereas multiple individual factors will contribute to the outcome of a translocation, transfer-related mortality (i.e. loss of life as a direct result of the capture/transfer/release processes) has a

significant negative impact on potential population establishment as any reduction in the number of initial founders reduces the likelihood of population persistence (Griffith *et al.* 1989). The capture and holding phases of a translocation are known to cause moderate to high levels of stress for most translocated individuals (Groombridge *et al.* 2004, Dickens *et al.* 2009, Adams *et al.* 2010, Parker *et al.* 2011) and the cumulative effects of stress can lead to reduced immune defence (McEwen 1998), and metabolic or behavioural crises (Dickens *et al.* 2009, 2010). The use of inappropriate capture, holding or release methodologies can exacerbate this problem (Parker *et al.* 2011), leading to high transfer-related mortality. Unfortunately, the species-specific methods and outcomes of many translocation attempts are not published (Parker *et al.* 2011), consequently reintroduction biologists have been emphasising the need for publication of both methods and results of translocations, regardless of the (positive or negative) outcome (Sutherland *et al.* 2004, Seddon *et al.* 2007, Armstrong and Seddon 2008, Parker *et al.* 2011).

The immediate post-release period (i.e. the establishment phase) produces its own set of stressors. Post-release effects could include ongoing chronic stress following transport and release (Dickens *et al.* 2010, Parker *et al.* 2011), stress associated with the arrival in novel environments (Dickens *et al.* 2009), and/or novel social interactions (Tavecchia *et al.* 2009), as well as Allee effects resulting from establishing populations at small initial sizes (Deredec and Courchamp 2007). These post-release stressors could also be compounded by initial responses to ongoing negative impacts such as inadequacies in the available resources (Armstrong *et al.* 2007, Bouzat *et al.* 2009), local competition (either intraspecific or interspecific) (Griffith *et al.* 1989), or predation (Lovegrove 1996; Fischer and Lindenmayer 2000). Losses during establishment are common and can further reduce the number of founders available to contribute to population growth and persistence (Lloyd and Powlesland 1994, Mumme and Below 1999, Reinert and Rupert 1999).

Small populations are susceptible to the effects of inbreeding, demographic stochasticity and environmental stochasticity (Jamieson *et al.* 2007, Jamieson 2011, Armstrong and Reynolds 2012), therefore the long-term viability of small founder populations is not assured. Reintroduction biologists advocate decision-making based on reliable and appropriate data collection, and robust modelling of population growth parameters (Armstrong and Reynolds 2012). Modelling procedures can be used to address many specific management options, including requirements for supplementary transfers (e.g. Armstrong and Ewen 2001), predator control (Armstrong and Davidson 2006; Armstrong *et al.* 2006), and nest site or supplementary food provisioning (e.g. Armstrong *et al.* 2002, 2007). Monitoring and modelling of vital rates, including survival and reproduction, both during and following the establishment phase, is crucial for accurate reporting on the outcome of translocations, particularly for small establishing populations (Armstrong *et al.* 2006, Armstrong and Reynolds 2012, Nichols and Armstrong 2012).

This study reports on the transfer design and establishment of the first translocation of the North Island subspecies of an endemic New Zealand passerine, the Rifleman (Acanthisitta chloris granti). The Rifleman (Acanthisitta chloris) is one of only two remaining species within the ancient New Zealand wren family (Acanthisittidae) (Sibley and Ahlquist 1990). Whereas the family originally consisted of seven species, five are now extinct. Both the North Island and South Island subspecies of Rifleman have been described as locally common. However, decreasing population sizes and increasing population fragmentation mean that the North Island subspecies is becoming increasingly threatened (Robertson et al. 2007). It is almost extinct throughout large areas of the North Island, and is now described as locally threatened or extinct in some regions (Robertson and Heather 1999). With decreasing habitat and the presence of pest species causing significant impacts on declining numbers of individuals (Clout and Gaze 1984, Lovegrove 1996, Holdaway 1999), conservation sites where intensive pest control and retention and restoration of native environments occurs are integral to the long-term survival of the subspecies. As the Rifleman occupies an important ecosystem niche as the smallest native insectivore (5-8 g) (Higgins et al. 2001), reintroduction efforts are considered important in addressing both species persistence and ecosystem function.

In 2003, the first translocation of South Island Rifleman *Acanthisitta chloris chloris* moved a small population from Codfish Island to the mammalian predator-free Ulva Island near Stewart Island. This translocation experienced high mortality during transfer, but the project was successful in establishing a continually viable breeding population, and provided several key recommendations regarding future transfer methodology for the rifleman species (Leech *et al.* 2007). In particular, Leech *et al.* (2007) recommended reduced holding times, the separation of individuals from different family groups, and the supply of food and water during holding. In 2008, a privately funded and managed mainland (i.e. non-insular) sanctuary was approved as a recipient site for the first translocation of the North Island Rifleman, providing an opportunity to apply the recommendations provided by Leech *et al.* (2007). Following three translocations from 2008 to 2010, we investigated whether implementation of these recommendations resulted in the anticipated reduced transfer-related mortality. We report on the revised transfer methodology, details of the monitoring and its outcome, and provide a quantitative assessment of the population's medium-term viability.

Methods

Study area

The source site for translocation was the Boundary Stream Mainland Island (BSMI), located within the Maungaharuru range within the Eastern ranges of the North Island of New Zealand (39°06′S, 176°48′E). BSMI is an 800-ha block of native forest that has been managed as a 'mainland island' site (i.e. a defined area typically protected by intensive invasive-mammal management) by the New Zealand Department of Conservation (DOC) since 1996. The site was selected as the most appropriate source location for two reasons; firstly, Rifleman occur at high densities within the intensively managed site and the source population was predicted to recover in numbers swiftly after removal of the translocated birds. Secondly, the reserve is in close geographic proximity to the Cape Kidnappers peninsula, resulting in ease of physical access to, and familiarity with the area by catchers, and shorter transportation times.

The recipient site was the Cape Kidnappers and Ocean Beach Wildlife Preserve (CKOBWP), located on the Cape Kidnappers peninsula in the Hawke's Bay region of the North island of New Zealand, approximately 50 km south-east of BSMI (39°40′S, 177°02′E) (Figure 1). CKOBWP is a privately-funded conservation initiative on private land that aims to restore the peninsula with native flora and fauna characteristic of the region's coastal system. Management of the site includes extensive mammalian pest control through trapping and poisoning, the maintenance of a 9.6-km predator-proof fence which spans the neck of the peninsula, and intensive reforestation efforts. A restoration plan has been developed to guide the reintroduction of native species to the peninsula, and the Rifleman was identified as one of four non-endangered endemic forest bird species absent from the area when the project began in 2007. Rifleman are considered likely to have once been present within the vegetated areas of the peninsula but have been absent for an unknown period of time, most likely as a result of predation and deforestation. As Rifleman are considered poor dispersers, it was also deemed unlikely that they would naturally recolonise the forested areas of the peninsula, despite the presence of wooded tracts of habitat, the reforestation effort, and the newly established maintenance of low mammalian predator numbers.

Before release, 130 artificial Rifleman nest-boxes were installed throughout the core area of the preserve where the birds were to be released and were expected to settle. The nest-box design was based on that of Gray (1969) and Sherley (1994), and was known to be used by other populations of Rifleman.

Translocation methodology

One week before catching, Rifleman calls were recorded from the source site for use as a lure during catching. Recorded calls were amplified using the program Audacity (Sourceforge.net) and edited into digital sound tracks for playback. Rifleman were targeted for capture during 28–31 January, 7–21 February and 20–23 September 2008. A supplementary transfer was carried out in

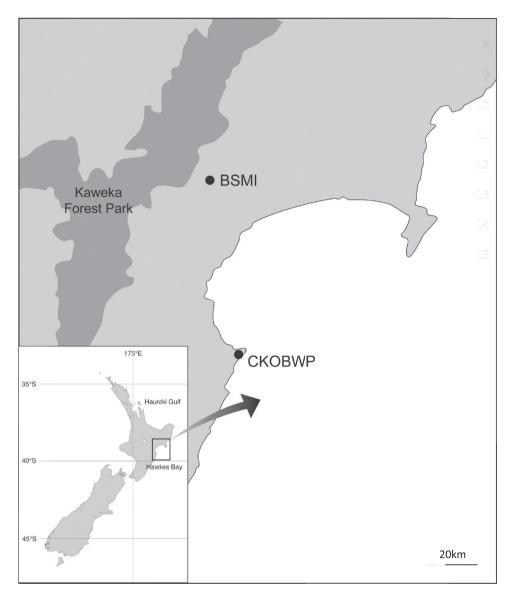


Figure 1. Location of source (Boundary Stream Mainland Island/BSMI) and recipient (Cape Kidnappers Preserve/CKOBWP) sites of the Rifleman translocation.

February 2010 using the same source and recipient locations. Rifleman were caught only on fine days and during daylight between 09h00 and 16h00. Several 25-mm gauge mist nets were positioned in known territories and playback of local Rifleman calls was used to lure Rifleman into the nets. Captured individuals were placed in black cotton holding bags and taken to a central processing site where they were physically examined, banded, weighed, and visually sexed from their dichromatic plumage, before being placed into individual small (210 mm x 150 mm x 150 mm) plywood holding/transfer boxes. The presence of juvenile plumage was also noted. Boxes were ventilated with small holes and contained perches, food, and water. Meal worms were provided *ad libitum* as a food source during transfer. Following recommendations from Leech *et al.* (2007),

only one Rifleman was placed into each holding box and only Rifleman from the same family group were held within calling distance of each other (Table 1). Also following the recommendations of Leech *et al.* (2007), and with permission from a certified veterinarian, Rifleman were not disease screened during the transfer process to avoid prolonged handling and associated stress.

All Rifleman were transported and released on the same day of capture and time from capture to release did not exceed five hours. Water bowls were removed from boxes prior to transfer. Rifleman were either flown by helicopter to the release site (transfer time approximately 20 min) or were driven to the site by vehicle (transfer time approximately two hours). Three release sites connected by contiguous habitat were used (located a maximum of 1.5 km apart). Releases took place no later than 16hoo to allow birds to settle and feed before nightfall.

Post-release population establishment and persistence

The forested area surrounding the release site was surveyed once each breeding season for three years following the initial release. Surveys involved walking along the tracks and lines cut for predator control access that span the preserve in a grid structure, and playing lure calls at regular intervals of 50 m. Any individuals heard or seen were followed and identified from their coloured leg bands; general home range locations, breeding partners, and nest locations were also identified. No individuals recorded as absent in one breeding were detected as present in a subsequent breeding season. We therefore assumed detection probability to be 100%; individuals not recorded were assumed to have died or dispersed outside the preserve.

Most females identified during surveys were subsequently monitored throughout the breeding season, allowing reproductive success to be estimated by detecting juveniles from their calls, which are loud and distinct (Higgins *et al.* 2001). As juveniles do not reach independence until up to five weeks following fledging (Sherley 1994), and remain in close contact with parents before independence (Sherley 1994, Higgins *et al.* 2001), we were confident that observations of juvenile numbers were an accurate indicator of reproductive success. Fledglings are distinguishable from adults based on the speckling on the breast (Higgins *et al.* 2001). Nest-boxes were checked each breeding season to assist in the detection of active nests.

Population modelling

We analysed the population data using an integrated approach in which survival, reproduction, and population dynamics were modelled simultaneously within a Bayesian hierarchical framework. The main advantage of this approach is that uncertainty in parameter estimation is automatically propagated into population projections (Besbeas *et al.* 2005, Barker *et al.* 2009, Kéry and Schaub 2012), meaning the precision of those projections accurately reflects the limitations of the data. The code was written in OpenBUGS (Spiegelhalter *et al.* 2003, Lunn *et al.* 2009).

We used a two-stage female-only model with a pre-breeding census (Figure 2). This model had four parameters: annual survival probability of first-year adults (S_1) , annual survival probability of older adults (S_2) , mean number of young fledged per female per year (R), and probability of a juvenile surviving to the next breeding season (S_j) . The recruits were assumed to have a 50% probability of being female, with the sexes assumed to have equal survival probabilities. This model structure reflected

Table 1. Comparison of translocation strategies/methods used for the Ulva Island Rifleman translocation compared to the CKOBWP translocation. Data for Ulva Island are given in Leech *et al.* 2007

Technique	Ulva Island	CKOBWP
Catch Times Holding time Holding associations	o7h00–21h00 Up to 5 days Mixed groups held together in aviaries	09h00–16h00 Up to 5 h Held in individual boxes. Families beyond audible range.

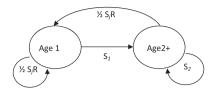


Figure 2. Life cycle modelling diagram for the female-only population model used for North Island Rifleman reintroduced to CKOBWP. S_1 and S_2 are the annual survival probabilities of a first-year adult and older adult respectively, R is the mean number of young fledged per female, and S_1 is the probability of a fledgling surviving to the next breeding season.

prior knowledge of the species' life history, including data showing low survival after the first year (Sherley 1985, 1993).

Adult survival probabilities were estimated from surveys conducted in each of the first three breeding seasons, with birds included in the data set only if they survived to the first breeding season. We modelled survival using the state-space formulation of the Cormack-Jolly-Seber model (Kéry and Schaub 2012) but found that we needed to assume 100% detection for all parameters to be estimated well (this was a reasonable assumption; see above). Age classes (first-year or older) were known in most cases, but in the first breeding season were known only for two females that had had juvenile plumage at the time of release. Consequently, the unknown age classes were modelled as missing values (Carpenter and Kenward 2013). The mean number of juveniles per female was estimated by sampling the numbers of young fledged by each monitored female each year from a Poisson distribution. Juvenile survival was modelled by sampling the number of recruits found in the second and third breeding seasons from binomial distributions, where the number of trials was the total number of juveniles produced in the previous season. However, because two females were not monitored in the second season, the total included missing values sampled for these two females. In addition, it was unclear whether unbanded birds found in the third season were recruits or surviving unbanded adults from the second season, so this uncertainty was also modelled.

We derived the population's finite rate of increase (λ) from the 2 x 2 Leslie matrix

$$\begin{bmatrix} f & f \\ S_1 & S_2 \end{bmatrix}'$$

where $f = \frac{1}{2} S_j R$. Solving for λ under a stable age distribution gives

$$\lambda_s = \frac{f + s_2 + \sqrt{(f_1 - s_2)^2} + 4fs_1}{2}.$$

We simultaneously obtained probability distributions for the projected number of females for 10 years after translocation, and these incorporated demographic stochasticity as well as parameter uncertainty. Demographic stochasticity in reproduction was simulated by sampling the numbers of young fledged each year from Poisson distributions with mean RN_t , where N_t is the number of females, and demographic stochasticity in survival and sex allocation were simulated by sampling the numbers of second-year adults, older adults, and female recruits from binomial distributions with probabilities S1, S2 and $V2S_j$ respectively. We used uninformative priors for all parameters and based posterior distributions on 10,000 samples after discarding a burn-in of 1,000 samples.

Results

Capture, transfer and release

A total of 86 Rifleman were caught during the 2008 (46) and 2010 (40) translocations (Table 2). Of these, 38 (21 males, 14 females, three unknown sex) were transferred in late January/early

Table 2. Number of mortalities (% in parentheses) at different stages of the translocation process for the Ulva Island and CKOBWP Rifleman translocations. Data for Ulva Island are given in Leech *et al.* 2007. CKOBWP results are separated according to translocation date on the bottom line (2008/2010).

	Caught	Died in aviary	Died in transfer box	Died during transport	Died at release	Released successfully
Ulva Island	58	14(24%)	6 (10%)	6 (10%)	2 (4%)	30 (52%)
CKOBWP	86	NA	1 (1%)	1 (1%)	1 (1%)	83 (97%)
(2008/2010)	(46/40)		(1/0)	(0/1)	(1/0)	(44/39)

February 2008, 8 (five males, three females) were transferred in September 2008, and 40 (15 males, seven females, 18 unknown sex) were transferred in February 2010 (Table 2). Most had adult plumage when captured, indicating they were over three months of age; in turn, five males and three females were judged to have juvenile plumage. All transferred Rifleman were within the normal weight range (Higgins et al. 2001), with females on average 6.7 ± 0.8 g and males 6.1 ± 0.8 g. All individuals survived capture and handling. Three individuals are considered to have died due to the transfer process. One individual did not survive the transfer and was found dead in the transfer box upon arrival, presumably from stress associated with handling and holding. An additional bird died shortly after arrival at the release site while still in the transfer box, and this death is also considered a result of the transfer. One individual was released alive but found dead several hours later and is considered to have died as a result of tail feather loss during capture and handling. All other individuals survived the transfer, regardless of the method of transportation (helicopter or vehicle). However, individuals that were transported via helicopter were noticeably more alert and dispersed from boxes in a faster timeframe than those moved by vehicle. Food was an important resource during transfer, as some birds consumed all available food supplied to them (although this was not the case for all individuals, regardless of the mode of transportation).

Post-release establishment

Eleven of the 44 (25%) individuals successfully released in 2008 were found in the preserve in the first (2008–2009) breeding season, comprising six males and five females. Seven of the 39 birds (18%) transferred in 2010 were found in the following breeding season. Therefore, 22% of the birds remained in the preserve and survived from the transfer process up to their first local breeding season, assuming 100% detection.

Dispersal and pair associations

Following release, individuals settled into territories within 500 m of the release sites. Founders appeared to have paired by the first breeding season, and all detected individuals were found in breeding units, typically consisting of one male and one female. One male appeared to be associating with two different females within the same area early in the first breeding season, but was not seen later in the season and is not considered to have contributed to the breeding population. Four breeding territories were located in both the first (2008–2009) and the second (2009–2010) seasons. Seven breeding territories were located in the third (2010–2011) season. Individuals appeared to maintain pair bonds throughout the winter, breeding with the same partner in subsequent breeding seasons, unless that partner disappeared. Offspring also appeared to establish territories with boundaries adjacent to the release site and to currently occupied territories, although a single male established a territory alone at a distance of 1.7 km from all other territories. Offspring born at the release site were observed to pair and establish territories almost immediately following independence. In the third season only one of the seven pairs located consisted of two first-year birds, whereas three first-year birds paired and bred with founders.

Survival and reproduction

Of the 11 birds (three first-year, eight age unknown) found in the first breeding season, six were found in the second breeding season, and two of these found in the third breeding season. These data gave estimated survival probabilities of 0.56 (SE 0.12) and 0.39 (SE 0.11) for first-year and older adults, respectively.

The four pairs with monitored breeding attempts in their first breeding season produced 10 fledglings (2, 2, 3, 3), two pairs with breeding attempts monitored in the second breeding season produced six fledglings (3, 3), whereas the other two pairs were not monitored sufficiently to accurately determine the number fledged; four pairs present in the third season produced 10 fledglings (3,4,1,2), with an additional three pairs not monitored. Overall reproductive success was therefore estimated as 2.39 (SE 0.47, n = 10) juveniles per female per year. The estimated 21.1 (SE 2.3) fledglings produced in the first two breeding seasons (SE 2.3) resulted in a total of six recruits, giving an estimated juvenile survival probability of 0.31 (SE 0.10).

The parameter estimates above result in an estimated finite rate of increase (λ) of 0.83, with a 95% credible interval ranging from 0.52 to 1.19. Starting from seven females in the third breeding season, population projections incorporating demographic stochasticity as well as estimation uncertainty produced a median population of 0 females after 10 years with an upper 95% prediction interval of 33 (Figure 3).

Discussion

Translocation methodology

Following Leech *et al.*'s (2007) documentation of the first translocation of Rifleman, which experienced a high level of transfer-related mortality, we sought to assess whether the implementation of their recommendations would result in a lower level of mortality during transfer. Leech *et al.* (2007) specifically recommended implementing reduced holding times, separation of different family groups, and an allowance for feeding time in the morning before capture and the afternoon following release. The adoption of these recommendations resulted in a transfer survival rate of 97% compared to the 52% for the previous Ulva Island translocation.

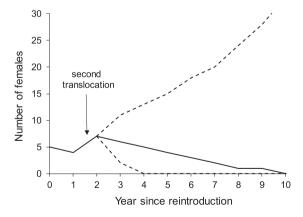


Figure 3. Distribution of population projections for the CKOBWP rifleman population. Projections are from a stochastic spreadsheet model constructed using data collected in the first three years after reintroduction (Years 0,1,2), and projections incorporate uncertainty in all population parameters. The solid line shows the predicted median number of females and the dashed lines show 95% prediction intervals.

Mortality specifically during the capture, holding and release phases of the transfer process was significantly decreased in the CKOBWP translocation compared to the Ulva Island translocation, with a reduction in mortality from 48% to 3%. While it is possible that alternative factors related to geography, genetics, or ecology, might explain some of this improved survival between the South and North Island translocations, the changes in holding social associations and times are likely to be major components of this reduced mortality. Several studies have demonstrated that the stress response to holding and transfer during the translocation process can be substantial for some species (Groombridge et al. 2004, Dickens et al. 2009, Adams et al. 2010, Parker et al. 2011). In a review of translocation capture and holding methodology, Parker et al. (2011) state that the key factors in the design of effective capture and holding methods include minimising stress caused by inefficient capture methods, and reducing enclosure changes. Dickens et al. (2009) also found that the holding and captivity period contributes most to the overall stress syndrome experienced by translocated animals. Whereas the Ulva Island translocation required two separate capture episodes, with birds held temporarily in aviaries, the CKOBWP translocation used only a single handling episode and a single enclosure (individual transfer boxes). The separation of Rifleman into individual holding boxes also appeared to be an effective technique for minimising the stress associated with forced interaction between territorial individuals. Leech et al. (2007) suggested that the losses associated with the holding phase of the transfer were the result of highly aggressive territorial interactions between non-familial individuals who were forced to share the same enclosures. Although best-practice holding methodology for avian translocations may be to separate individuals in aggressive, territorial species, the need for separation in territorial species appears to depend on each species' individual tolerance to conspecifics. For example, both the territorial Saddleback Philesturnus carunculatus and Hihi Notiomystis cincta can be successfully held in collective aviaries (Armstrong et al. 1999, Taylor and Jamieson 2007), whereas New Zealand Robins Petroica spp., Fernbird Bowdleria punctata vealeae (Parker et al. 2011) and Rifleman (this study) all appear to require and benefit from individual holding enclosures. This is particularly noteworthy as the Rifleman is not described as a highly territorial species and will tolerate territory incursion by conspecifics in the wild (Campbell 1990, Higgins et al. 2001). Energetic requirements might also be a significant factor to consider when determining appropriate holding times. Rifleman, especially given their small size, are considered to be highly metabolically demanding, and spend a very high percentage of their time foraging (up to 82.5%) (Sherley 1985, Lill 1991). Therefore, longer holding times might be responsible for increased mortality as a direct result of a lack of sustenance. While food was provided during both the Ulva Island and CKOBWP translocations, individuals varied in their consumption during the CKOBWP translocation (Tamsin Ward-Smith pers. obs.). As the stress response to capture and holding results in increases in both heart rate and energy mobilisation in birds (Parker et al. 2011), we suggest that some individuals might not be feeding enough during holding to compensate adequately for the increased metabolic rate produced by stress.

Post-release population establishment and persistence

While the revised transfer methodology described here appears to have decreased transfer-associated mortality significantly, the re-sighting of translocated individuals post-transfer was low, indicating high post-release mortality and/or dispersal. Numerous reintroduction studies have noted considerable mortality following translocation (Musil *et al.* 1993, Sarrazain and Legendre 2000, Armstrong and Ewen 2001, Tavecchia *et al.* 2009). Translocated birds can be vulnerable due to post-release experiences in novel environments and with competitors and/or predators (Dickens *et al.* 2009, Parker *et al.* 2011).

The habitat at CKOBWP is a regenerating environment with patchy areas of mature forest, surrounding dry river-beds, and is likely to be suboptimal in comparison to the mature forest habitat at the source site, BSMI. Rifleman occupy mature forest in most natural populations (Higgins *et al.* 2001, Robertson *et al.* 2007), and data from Rifleman translocated to Ulva showed biased dispersal

toward mature forest areas (Mitchell 2004). The dispersal behaviour of the Rifleman translocated to CKOBWP appears to have followed a similar pattern, with fidelity to the release sites and a concentration of territories around mature trees. It is possible that some translocated Rifleman are attempting longer-distance dispersal in search of preferred areas of habitat, which could contribute to the low number of observed survivors within the monitored population. The dispersal of a lone male Rifleman 1.7 km from the release site provides support for the idea that dispersal might be at least partially responsible for apparent lower survival in the monitored population.

Competitive interactions are considered unlikely to be responsible for post-release mortality and dispersal in the CKOBWP Rifleman population. Rifleman are infrequently subjected to aggression from inter-specific competitors or aggressors in natural South Island (Gray 1969, Higgins *et al.* 2001) and North Island populations. Aggressive interactions with both native and exotic species have been observed in the CKOBWP population (Withers 2009, Withers, pers. obs), however these interactions do not appear to commonly result in injury. Additionally, potential inter-specific competitors and aggressors are at low densities at the CKOBWP site. Predation is also considered unlikely to have played a significant role in post-release mortality. Predator monitoring at the release site shows that the exotic mammals, which are likely to be the main threats to Rifleman, are kept at low levels (Tamsin Ward-Smith, unpublished data).

Stress associated with the novelty of new environmental cues might be acting to increase the post-release mortality of translocated Rifleman (Dickens *et al.* 2009), and ongoing stress as a result of the transfer itself might also be a factor (Dickens *et al.* 2010, Parker *et al.* 2011). Although the adjustment of translocation techniques described here has reduced transfer-associated mortality for Rifleman, it is likely that the process of translocation per se still represents a significantly stressful event for transferred birds. The effects of such chronic and post-event stress can manifest in numerous ways including reproductive suppression, compromised immune responses and altered behaviour or physiology (Dickens *et al.* 2010), and may increase vulnerability to potential threats present at the release site and ultimately affect translocation success (Parker *et al.* 2011).

Lastly, survival might be affected by a normal trend toward higher mortality over winter. Rifleman populations experience winter declines in natural populations, with losses of up to 35%; over-wintering mortality is sex-biased, with the number of females declining significantly more than that of males (41% compared to 29%) (Lill 1991), indicating that females incur higher overall annual losses than males. Natural attrition of older birds may also explain the higher post-release mortality found in this transfer, as many adult birds were of unknown age.

Population modelling

Using monitoring data collected during the three years following release, our population model projected potential population growth in the medium term – i.e. for the 10 years following translocation. This model indicates that, despite the increase in transfer survival due to improved translocation methodology, the population has a low probability of survival in the medium term. Griffith et al.'s (1989) comparative study suggests that on average up to 80 founders are needed to maximise the probability of population establishment. Therefore, it is possible that the low initial number of surviving individuals at the first breeding season is implicated in the negative population projections. However, New Zealand translocations often succeed with only a very small number of initial founders (Armstrong and McLean 1995, Byrne 1999). Despite ongoing concerns regarding inbreeding and the subsequent extinction risks in small founder populations (Taylor et al. 2005, Frankham 2005, Jamieson et al. 2006), some populations persist for decades despite having fewer than 10 founding individuals (e.g. Ardern and Lambert 1997). Small founding populations can recover rapidly after release with high rates of survival and reproduction because of competitive release, or due to the effects of reduced density when reproduction or juvenile survival is density-dependent (e.g. Komdeur et al. 1995, Westemeier et al. 1998, Armstrong and Ewen 2002, Taylor et al. 2005, Bouzat et al. 2009).

The low rates of juvenile survival and reproductive success found in our study also contribute to the population's high likelihood of extinction in the medium to long term. Our estimate of juvenile survival (31%) is substantially lower than the estimated juvenile survival rate of 53–80% for the successfully established population of Rifleman translocated to Ulva Island (Leech *et al.* 2007). Our estimates of reproductive success are also somewhat lower than the maximum reproductive potential of Rifleman which can produce between two and five eggs per clutch and lay up to two clutches per season (Higgins *et al.* 2001). Reported first clutch sizes in natural populations of the South Island subspecies have ranged from 4.4 (Kowhai Bush) to 3.8 (Dunedin) (Gray 1969, Sherley 1985) and are as high as 4.5 young per clutch in the Orongorongo Valley, the only North Island site with comparative data (Gaze 1978).

As translocations can sometimes result in a reduction in reproductive success in the years immediately following transfer (e.g. Armstrong and Ewen 2002), we estimated that reproductive success based on actual observed fledged clutch sizes within our population, resulting in a lower but more accurate reproductive rate estimate compared to Leech et al. (2007) who estimated clutch size (2.7 young per clutch) based on a previous study on a distinct and nontranslocated population. In line with the Ulva Island projections, we also based our model on a single clutch per season which was consistent with our observations. It is possible that the reproduction rates found in our population are lower than normal due to Allee effects. Allee effects refer to any negative effects on survival or fecundity in relation to the reduced population size and therefore include both loss of genetic diversity as well as declines in relation to adjusted social dynamics (for example) (Deredec and Courchamp 2007). Reproductive rates could be affected by the inevitable alteration and reduction in social group size and make-up as a result of translocation; due to a lower partner detection rate at low density; or a combination of both of these factors (Deredec and Courchamp 2007, Armstrong and Wittmer 2011). As helpers can increase reproductive success in some cooperative species (e.g. Ridley 2007), this might be particularly important for species which employ cooperative breeding strategies, such as the Rifleman (Sherley 1990). Research on the South Island sub-species of Rifleman indicates that the benefits of helping may include an increase in juvenile recruitment (Preston et al. 2016). As no cooperative breeding was observed at the CKOBWP site during our study, this might be one factor affecting reproductive or recruitment rates. The release of individuals at two different sites could have increased the likelihood of Allee effects affecting reproduction in the CKOBWP population. One individual was observed moving between the two release locations, but the majority of monitored individuals showed strong fidelity to their respective release site and chose breeding pairs from those released within the same site. In small populations, the likelihood of encountering potential partners is reduced, decreasing potential reproductive rates in the population (Deredec and Courchamp 2007). We recommend using a single release site for future translocations of Rifleman when releasing small founder populations.

Our investigation suggests that following the 2008 and 2010 translocations, the CKOBWP Rifleman population is unlikely to survive in the medium-long term, but the population model predictions also contain high levels of uncertainty. This model demonstrates the importance of incorporating the effects of demographic stochasticity as well as uncertainty in parameter estimates when producing population projections from small population sizes or sparse data sets. As demographic stochasticity can contribute to post-release effects (Deredec and Courchamp 2007), population models that do not incorporate these levels of uncertainty may overestimate the likelihood of population persistence, leading to inappropriate decisions regarding future management options (Armstrong and Wittmer 2011). Questions relating to population establishment in terms of the size and make-up of founder groups are most effective when incorporating known reproductive and survival rates into population models (Armstrong and Seddon 2008). Given the scarcity of data on vital rates for small populations of managed species, monitoring and reporting are therefore vital to the production of accurate models and effective long-term management decisions (Nichols and Armstrong 2012).

Conclusions and recommendations

Our test of the efficacy of Leech *et al.*'s (2007) recommendations resulted in significantly improved transfer survival compared to previous transfers of Rifleman. Our key recommendations are to avoid prolonged holding and transfer times, to allow adequate feeding time both prior to and following capture and transfer, to ensure individuals and family groups are kept separate during holding to reduce territorial aggression and the use of a single release site when translocating small numbers of birds. These recommendations will be important also for any translocations involving territorial and highly metabolically demanding species worldwide. These adjustments to the transfer methodology resulted in 97% of birds surviving the transfer and release phase, yet the establishment phase experienced higher losses. We suggest that Rifleman at CKOBWP are affected by post-release effects, including high over-winter mortality and an increased dispersal rate from the release sites in the locally patchy woodland habitat-matrix. Rifleman dispersal at this site might be increased due to a lack of familiarity with the environment in addition to an increased likelihood of dispersal outside the protected/monitored areas in mainland release sites compared to island release sites.

The population viability model employed here predicted a negative population trend for the population in the medium term and implies a low probability of success for this population. However, uncertainty in our estimates is high due to the small population size and missing subsets of demographic and monitoring data. The current status of the CKOBWP Rifleman population is unknown. A further transfer of Rifleman was carried out in 2011 for which no data are available meaning an updated model of future population viability is not possible. Anecdotal reports of a small number of individuals still present indicates that there may be a very low-density breeding population still present at the site. This study demonstrates the importance of incorporating demographic stochasticity and uncertainty in vital rate estimates when producing population models for small reintroduced populations and projects with sparse data. We strongly recommend the collection and reporting of frequent monitoring data following any translocation, allowing more accurate model development and population projections.

Author contributions

TW-S planned and carried out the translocation that forms the basis for this manuscript. SJW, MEH, SP and TW-S founded the idea to collaborate on collection of monitoring data in order to answer the hypothesis proposed by this manuscript. SJW and TW-S monitored the population and collected survival and reproductive data, with data analysis being performed by SJW and DA. SJW and DA wrote the manuscript with input from TW-S, SP and MEH.

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