CrossMark

Can translocations to islands reduce extinction risk for reptiles? Case studies from New Zealand

D.R. Towns [a,b,*], K.A. Miller [c,d], N.J. Nelson [d], D.G. Chapple [d,e]

[a] Department of Conservation, Auckland 1145, New Zealand
[b] Institute for Applied Ecology New Zealand, School of Applied Sciences, Auckland University of Technology, Private Bag 92019, Auckland 1142, New Zealand
[c] Department of Infrastructure Engineering, The University of Melbourne, Parkville, Victoria 3010, Australia
[d] Allan Wilson Centre for Molecular Ecology and Evolution, School of Biological Sciences, Victoria University of Wellington, Wellington 6140, New Zealand
[e] School of Biological Sciences, Monash University, Clayton 3800, Victoria, Australia

ARTICLE INFO

ABSTRACT

Globally, one in five reptile species is threatened with extinction, with invasive species a leading cause of extinction risk. Translocations could alleviate the risk of extinction through the establishment of populations in locations from which invasive predators have been removed. But do translocations represent a viable strategy for reptile conservation? We investigate the numerical and genetic outcomes of translocations of reptiles as reintroductions to islands cleared of introduced mammals around New Zealand. These reintroductions included nine populations of tuatara (*Sphenodon punctatus*), ten populations of six species of geckos and 24 populations of 12 species of skinks on a total of 24 islands. Reintroduced populations are often relatively small, which exposes them to associated demographic and genetic problems. We compared criteria for success based on abundance with available genetic data for four species of reintroduced reptiles. Three populations of skinks showed some loss of genetic heterozygosity but have nonetheless met most criteria for numerically viable populations. Whether loss of genetic variability might have long-term consequences for persistence is unclear because the genetic basis for population viability is still debated. We found that the success of reintroductions can be influenced by complex interactions between numerical, genetic and administrative constraints on project design. We thus suggest that obtaining data on the outcomes of reptile recovery will require managers to avoid mixing populations for pre-emptive genetic rescue, and a commitment to long term ecological and genetic studies.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Conservation translocations involve the deliberate movement of organisms from one site for release into another with the intention of yielding a measurable conservation benefit (IUCN/SSC, 2013). Many translocations have been attempts to remove animals from harm. For example, translocations of birds to avoid or recover from threats posed by introduced predators have been practised in New Zealand for over a century (Saunders, 1995), with over 1100 translocations attempted and 41 species successfully established (Miskelly and Powlesland, 2013). Similarly, numerous mitigation translocations have been conducted to remove species in the path of development (Germano et al., 2015). An example is the Florida Gopher tortoise (*Gopherus polyphemus*), with hundreds of mitigation translocation attempts since the late 1980s (Germano et al., 2015). When translocations

are used for population restoration, two kinds of activities are recognised (IUCN/SSC, 2013). The first is reinforcement, when individuals are added to an existing population of the same species. The second is reintroduction, where organisms are released into those parts of their historic range from which they have been extirpated (e.g. Armstrong and Seddon, 2007).

In a recent review of the conservation status of the world's reptiles, Böhm et al. (2013) revealed that 20% of the global fauna is threatened with extinction. They also concluded that invasive species appear to raise the extinction risk on islands, with New Zealand as one example. Partly as a result of the effects of invasive species, the proportion of threatened species in the New Zealand reptile fauna (32%; Nelson et al., 2014) is higher than the global average. Invasive mammals have been eliminated from at least 104 islands within the New Zealand archipelago (Towns et al., 2013) in order to recover species otherwise faced with extinction or for ecosystem restoration (e.g. Towns and Atkinson, 2004). Reintroductions of reptiles have increasingly become part of these restoration activities with some of the earliest global attempts reported by Thomas and Whitaker (1995) and Towns and Ferreira (2001). However, concerns about the effectiveness of reptile translocations – including reintroductions — were raised by Dodd and Seigel (1991) and

* Corresponding author at: Department of Conservation, Private Bag 68 908 Newton, Auckland 1145, New Zealand.
E-mail addresses: dtowns@doc.govt.nz (D.R. Towns), kim.miller@unimelb.ac.au (K.A. Miller), nicola.nelson@vuw.ac.nz (N.J. Nelson), david.chapple@monash.edu (D.G. Chapple).

some of these concerns remain: translocations can be poorly monitored and conservation benefits may be unclear (Germano et al., 2015). Here we assess whether reintroductions of reptiles so far undertaken on islands in New Zealand are likely to reduce extinction risk faced by the fauna.

Because reintroduced populations are likely to begin with < 100 individuals (Wolf et al., 1996; Germano and Bishop, 2009), they share many of the risks associated with relict populations, which include restrictions on growth due to demographic or environmental stochastic problems. Demographic problems can include inappropriate social structure and Allee effects, when behaviour or dispersal of one sex impedes breeding. However, unlike relict populations, those reintroduced to islands are likely to have predetermined demographic structure, sex ratios (if adults) and release sites of known location. On the other hand, released populations may face environmental stochastic problems if release sites are so confined that they are vulnerable to localised catastrophes such as habitat loss or the effects of extreme climatic events (Shaffer, 1981).

An enduring problem for translocations has been a lack of consistently applied criteria to measure success. Dodd and Siegel (1991) proposed that translocations would be successful if the populations are self-sustaining and at least stable. However, Wolf et al. (1996) required successfully translocated populations to be self-sustaining and comprised of locally born animals. More recent authors (e.g. Cree, 2014; Miller et al., 2014) have proposed staged approaches, in which criteria such as those proposed by Dodd and Seigel (1991) represent early stages of the process of establishment, whereas those proposed by Wolf et al. (1996) apply when establishment is complete. None of these criteria consider the potential genetic outcomes of translocation, yet small populations face indirect genetic challenges such as inbreeding depression, which can lead to low fitness, low fertility and vulnerability to disease (Shaffer, 1981; Frankham, 2005; Miller et al., 2008; Jamieson, 2010, 2015). The genetic outcomes of reptile translocations have rarely been studied. One exception is a study of numerical and genetic effects of shifting fire regimes on a fragmented metapopulation of North American collared lizards (*Crotaphytus collaris*; Neuwald and Templeton, 2013). Genetic lessons provided by translocations and population fragmentation of other vertebrates are likely applicable to reptiles in part (e.g. Weeks et al., 2011), but unusual features of reptile biology require caution with uncritical extrapolations. For example, measures of reduced fitness in birds may be based on clutch size and embryonic survival (Jamieson, 2015). However, in many reptiles clutch size increases with body size, but may also fluctuate in response to environmental cues such as weather conditions and food supply (e.g. Cree, 2014). Compromised fitness in reptiles may thus be difficult to identify and in newly translocated populations could be masked if there are unconstrained food supplies in the new habitat.

Given the large number of island restoration projects and the relatively long history of reptile reintroductions in New Zealand, it is timely to now ask whether their potential for population restoration is being met and what lessons might be applicable elsewhere. In order to address these questions, we identify the number of reintroductions, focus on those with numerical and genetic data as case studies, and discuss the key questions and problems that these case studies reveal.

2. Methods

Reintroduction data were gathered from published sources, grey literature such as institutional (Department of Conservation) files, and our own unpublished material. The numerical and genetic outcomes of reintroductions could be influenced by growth rates and reproductive strategies, which we summarise for selected species below.

We have been directly involved in two groups of studies, which form the focus of our review. The first was for tuatara on islands off central New Zealand. This species shows extreme longevity (up to 100 years); slow growth to maturity (at least 10 years); intermittent breeding (average every 4–5 years), but with higher frequency (2 years) in some

northern populations; and low annual reproductive output (ARO) per female (1.3–2.3), where ARO is the number of eggs or young per female per year averaged across years (Cree, 1994, 2014). Ecological studies of reintroductions were conducted by Nelson et al. (2002, 2008). There have been no studies of the genetic effects of tuatara reintroductions because any offspring are only F1, cryptic and rarely recaptured. Instead, potential effects of the reintroductions were determined from genetic surveys of donor populations (Miller et al., 2009). Tuatara were genotyped at six or seven microsatellite DNA loci (depending on island origin) and amplified by PCR (Miller et al., 2009) using the assumption that variation at microsatellites was reflective of the entire genome.

The second group comprised *Oligosoma* skinks of northeastern New Zealand. On Korapuki Island (Mercury Islands; 36.66 S, 175.85 E), numerical and genetic data were obtained for three species, each of which has moderate longevity (20–30 years) and takes 2–3 years to reach sexual maturity, but they have variable ARO. Lowest ARO is for *Oligosoma whitakeri* (2.0) followed by *Oligosoma alani* (3.0) and *Oligosoma suteri* (3.7) (Towns, 1975, 1994). Ecological studies of progress with reintroductions were conducted annually for 10 years after each release by Towns (1994) and Towns and Ferreira (2001). Genetic studies of the skinks and their donor populations were conducted in the Mercury Islands 14–18 years after the lizards were released (Miller, 2009; Miller et al., 2009, 2011). Skinks were genotyped at up to 10 microsatellite DNA loci amplified by PCR as described by Miller et al. (2011).

We assigned the tuatara and those lizards with comprehensive post release data (including some without genetic data) to each of the four stages for successful reintroduction defined by Miller et al. (2014). The lizards included three additional species with which we had direct involvement in reintroductions: a fourth species reintroduced to Korapuki Island and two species reintroduced to Lady Alice Island (Marotiri Islands; 35.92 S, 174.73 E). The Miller et al. (2014) criteria are: 1) survival and growth of individuals—recapture of measured proportion of release propagules, increase in body mass, size or condition of individuals; 2) evidence of reproduction—detection of birth into translocated populations (excluding to those individuals gravid/pregnant on release); 3) population growth—captures exceed size of release propagule, evidence of second generation breeding, lambda >1.0; and 4) population viable—captures regularly exceed size of the release propagule, immature regularly observed, founder proportion small, negligible probability of extinction (e.g. through population viability analyses).

3. Results

3.1. Tuatara

Since 1995, tuatara have been translocated to 13 islands after eradication of invasive mammals. On four islands, tuatara were moved to secure facilities, either on the island (Hauturu/Little Barrier) or on the mainland (the remaining three), while Pacific rats (*Rattus exulans*) were eradicated. Juveniles from these islands that were raised in captivity were released as reinforcements to supplement the relict populations of adults (Table 1). Excluding the four reinforcements, tuatara have been reintroduced to nine islands (see also Cree, 2014). Five reintroductions were transfers direct from other wild populations (wild–wild). The remaining eight were either derived from or reinforced with tuatara hatched and raised in captivity (Table 1). The mean propagule size for tuatara reintroductions was 92.9 ± 42.6 (± SE) with the most frequently used propagule about 60 (Fig. 1). Despite cryptic behaviour and low ARO, post-release monitoring on seven islands indicates survival of at least some of the founding animals for up to 14 months and in three populations locally-hatched juveniles have also been reported (Cree, 2014). On Titi Island, monitoring 11 years after release, located 44% of adult and 28% of the founding juvenile tuatara as well as the first locally born juvenile (Cree, 2014). None of the populations

Table 1

Reptile reintroductions to islands cleared of introduced mammals in New Zealand; updated from Sherley et al. (2010) using data reviewed in [1]Cree (2014), and other data from [2]Anderson et al. (2015), [3]Baling et al. (2013), [4]Parrish (2008), [5]Bell and Herbert (2016), [6]Van Winkel et al. (2010), [7]Miskelly (2010); [8]Thomas and Whitaker (1995), [9]Towns and Ferreira (2001), [10]Baling et al. (2010); the very large number of juvenile tuatara for Whakatere-Papanui was the outcome of a research project; those marked [W] based on wild–wild transfers rather than animals raised in captivity; those marked [W/C] are a mix of wild and captive-bred; male (m): female (f) ratios given if known; threat status (in parentheses) is based on Hitchmough et al., in press with relevant categories: Threatened, Nationally Endangered (NE); At Risk, Declining (D), Recovering (Rec) and Relict (Rel); Not Threatened (NT).

Species and threat status	Location	Year began	Source island	Number	Status/notes
Sphenodontidae					
Sphenodon punctatus[1,2,3] (Rel)	Titi[W/C]	1995	North Brother	68	Adults (7m:11f) from wild and 50 juveniles from captivity
	Moutohora[W]	1996, 2008	Moutoki	30, 32	All adults (12m:20f) in 1996; reinforcement in 2008 by large juveniles and small adults (14m:16f)
	Matiu/Somes[W/C]	1998	North Brother	55	Included 30 juveniles from captivity
	Cuvier[W/C]	2001	Cuvier	30	Reinforcement, includes 17 juveniles from captivity
	Whakatere-Papanui	2003	Stephens	432	Included 333 juveniles raised in captivity
	Kawhitu[W/C]	2003	Kawhitu	15	Reinforcement, includes 9 juveniles from captivity
	Tiritiri Matangi[W]	2003	Middle	60	Adults (30m:30f)
	Red Mercury[W/C]	2006	Red Mercury	25	Reinforcement, adults and some juveniles from captivity
	Hauturu/Little Barrier[W/C]	2006	Hauturu /Little Barrier	140	Reinforcement, all juveniles raised in captivity
	Mayor[W]	2007	Karewa	30	Adults (15m:15f)
	Long	2007	North Brother	55	All juveniles raised in captivity
	Motuihe[W]	2012	Lady Alice	30	All subadults
	East[W]	2012	Stephens	44	Adults (25m:19f)
Diplodactylidae					
Dactylocnemis pacificus[4] (Rel)	Lady Alice[W]	1997	Pupuha	30	Adults (15m:15f)
D. sp. Matapia (D)	Motuopao[W]	1997	Matapia	41	Included 5 juveniles
Hoplodactylus duvaucelii[3,5,6] (Rel)	Mana[W]	1998–2001	North Brother	40	Adults (10m:20f; 10 subadults)
	Tiritiri Matangi[W]	2006, 2013	Korapuki	19	Adults (9m:10f); reinforcement release of 90 (composition unknown)
	Motuora[W]	2006	Korapuki	20	Adults (10m:10f) included 1 juvenile
Mokopiririkau granulates (D)	Matiu/Somes	2006	Wellington (mainland)	33	Composition unknown; some held in captivity
Naultinus manukanus (D)	Motuara[W]	1997	Arapawa	14	Included 3 juveniles
	Wakatere-Papanui[W]	2003	Stephens	44	Included 17 juveniles
N. punctatus[7] (D)	Mana[W/C]	1998–2005	Wellington (mainland)	47	Included 20 raised in captivity
	Matiu/Somes	2007	Wellington (mainland)	9	Composition unknown
Scincidae					
Oligosoma acrinasum[8] (Rel)	Hawea[W]	1988	Wairaki	40	Composition unknown
O. alani[9] (Rec)	Korapuki[W]	1992	Green	14	Included 2 juveniles
	Red Mercury[W]	1994	Atiu	30	Composition unknown
	Kawhitu[W]	1995	Atiu	30	Adults (2 m:11f:9unknown) and 8 juveniles
	Motuopao[W]	1997	Matapia	30	Included 3 juveniles
O. infrapunctatum[7] (D)	Mana[W]	2004	Stephens	40	Composition unknown
	Maud	2004	Stephens	40	Composition unknown
O. lineoocellatum[7] (Rel)	Mana[W]	1998	Matiu/Somes	50	Composition unknown
O. macgregori (Rec)	Lady Alice[W]	1997	Sail	39	Adults and 4 juveniles
	Whatupuke[W]	2000	Sail	30	Adults
O. sp. (D)	Ulva	2005	Stewart Island/Rakiura	62	Composition unknown
O. oliveri (Rel)	Korapuki[W]	1992	Green	25	Adults and 11 juveniles
O. ornatum (D)	Matiu/Somes	2006	Wellington (mainland)	31–37	Adults (8m:11f) and 6 juveniles plus unknown
O. smithi[10] (NT)	Motuora[W]	2006	Tawharanui (mainland)	40	Adults (24m:26f)
	Tiritiri Matangi[W]	2006	Tawharanui (mainland)	40	Adults (22m:21f) and 7 juveniles
	Motuihe[W/C]	2009	Tawharanui (mainland)	80	Composition unknown, 30 captive bred subadults and 50 wild
	East		East Cape (mainland)	250–300	Composition unknown
O. suteri[9] (Rel)	Korapuki[W]	1992	Green	30	Adults (10m:20f)
O. townsi[4] (Rec)	Lady Alice[W]	1997, 2005	Muriwhenua	30, 31	Adults: (15m:15f, 14m:17f)
	Whatupuke[W]	2002	Middle Stack	30	Adults (15 m:14f) and one juvenile
	Coppermine[W]	2002	Middle Stack	30	Unknown
O. whitakeri[9] (NE)	Korapuki[W]	1988	Atiu	28	Adults (8 m:5f) and 15 juveniles
	Red Mercury[W]	1994–5	Atiu	30	Adults (9m:5f:1unknown) and 15 juveniles
	Kawhitu[W]	1995	Atiu	30	Composition unknown

have progressed beyond the appearance of locally born young, which is the second stage of Miller et al. (2014). Furthermore, whether any of the locally born tuatara were progeny of females gravid on release cannot be determined.

Microsatellite analyses for three of the translocated populations of tuatara indicated that founders retained 84.2–100% of the allelic diversity of their source populations. Models of population viability also indicate that after 10 generations, populations with founder groups of
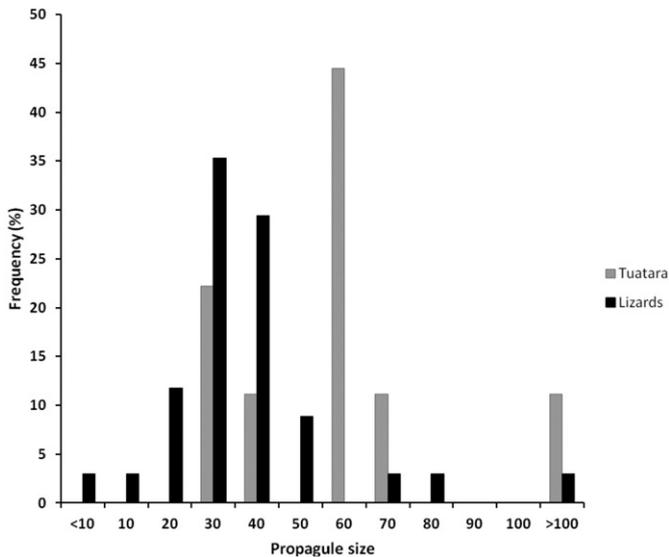
Fig. 1. Frequency of propagule sizes for populations of tuatara (n = 9) and lizards (n = 34) reintroduced to islands in New Zealand cleared of introduced mammals (reinforcements excluded).

about 70 individuals will likely retain a greater proportion of the heterozygosity and allelic diversity of both the source population and the founder groups themselves than smaller founder groups. However, little genetic benefit was added if founder group size was increased beyond this number (Miller et al., 2009).

3.2. Lizards

Since 1988, at least ten populations of six species of geckos, and 24 populations of 12 species of skinks have been reintroduced to 19 islands (Table 1). The largest number of species reintroduced to a single site comprised four species of skinks to Korapuki Island from neighbouring islands in the Mercury archipelago (Towns, 2002; Towns and Atkinson, 2004). The mean propagule size for lizards was 40.5 ± 6.7, with the most commonly used propagule of 30 (Fig. 1). Available data indicate that seven populations of geckos (70%) were wild–wild transfers as were 19 (79%) of skinks. No populations appear to have been solely derived from animals raised in captivity. Intensive post-release monitoring of the gecko *Hoplodactylus duvaucelii* indicated that 15 years after the release onto Mana Island (central New Zealand), founding adults were still present (Bell and Herbert, 2016), but population size had increased. The species may thus have reached Stage 4 of Miller et al. (2014; Table 2). Few other records other than re-sightings are available for the other five species of geckos, although Miskelly (2010) noted that none of the *Naultinus punctatus* released on Mana Island have subsequently been found.

Of the skinks reintroduced to islands, data on post release outcomes are available for seven of the 18 species (39%), representing 24% of all populations released. The most rapid establishment was of *Oligosoma acrinasum* on Hawea Island, which increased in number from 40 captured on Wairaki Island to >200 on Hawea within five years. However, these numbers may have been supplemented by natural over water dispersal from Wairaki to Hawea (Thomas and Whitaker, 1995). Surveys on Lady Alice Island 18 years after the release of *Oligosoma macgregori* and 10 years after the second release of *Oligosoma townsi* indicated that the new populations are at least stable. There was also apparent replacement of the *O. macgregori* population by locally born animals (B. Barr pers. comm.), since 62% of those released had natural toe loss, but the recent captures had all toes present. However, animals used for the first release of *O. townsi* on the island appear to have dispersed outside of the release area and have yet to be found (Parrish, 2008).

On Korapuki Island, capture data confirm earlier predictions of population growth from matrix models (Towns and Ferreira, 2001): the skinks *O. alani*, *O. whitakeri* and *O. suteri* reintroduced to the island now meet the criteria for establishment as viable populations based on numerical abundance (Table 2). Between 5 and 7 years of monitoring (respectively) were required to determine that each species had reached Stage 3 despite high post-release survival (>60%; Table 2). The most rapid population increase was for *O. suteri*, with an estimated 400 individuals 14 years after release (Miller et al., 2014). Unlike the random captures used for other species, adults were the only cohort used for *O. suteri* and these were intentionally biased to gravid females (10 males:20 females) in an attempt to maximise productivity (Towns and Ferreira, 2001). For a fourth species, *O. oliveri*, replacement of the founders appears complete (D. Towns unpublished data), but too few have been captured to confirm an increasing population. The latter species has not progressed beyond Stage 2 (Table 2).

Models of the genetic effects of the reintroductions on *O. alani* and *O. whitakeri* predicted heterozygosity loss of about 10% after 10 generations. The average loss of heterozygosity for the *O. whitakeri* population 20 years after release on Korapuki Island was 8% compared with 1% at 15 years for *O. suteri* (Miller, 2009). The effects of reintroduction varied according to propagule size and composition. For example, with 20 gravid females in the release group of 30 *O. suteri*, the effective population size (N_e) of the translocation propagule (30) was about 50 after several generations (Miller et al., 2011). Nonetheless, the population showed some evidence of a post-reintroduction bottleneck and, compared with the source population on neighbouring Green Island, a decrease in the proportion of rare alleles over time. After 4–5 generations, the rapidly expanding population on Korapuki had retained over 90% of the allelic diversity of the population on Green. In theory, reduced individual heterozygosity might be reflected in reduced levels of fitness. However, for *O. suteri*, there were no significant correlations between individual heterozygosity and performance measures based on sprint speed and dive duration (Miller et al., 2011).

3.3. Unforeseen and externally imposed problems

Propagule sizes for at least some species of lizards were based on decisions outside the control of those conducting releases. For example, in the Mercury Islands, release groups of 30 or less per donor island were imposed by reserve management committees concerned about potential damage to habitats and populations (D. Towns unpublished data). On the other hand, institutional priorities required that reintroduction attempts focussed on the rarest species (e.g. Towns, 1994). In the Marotiri Islands, traditional Māori guardians rejected requests to permanently mark the released animals using toe clipping. The corresponding strategy was to only release adults (including pregnant females), which meant that any young subsequently observed would represent local recruitment (Parrish, 2008; D. Towns unpublished data).

Some species appear to show idiosyncratic behaviour after release. On Mana Island, *H. duvaucelii* released into a forested area remained within 140 m of the release site for at least 15 years (Bell and Herbert, 2016). However, the same species on more northern islands moved widely, requiring surveys beyond the immediate release site (van Winkel et al., 2010). We also identified two populations that could not be detected after release (Table 1). One example was the first release of 30 *O. townsi* adults, which after release into bouldery habitat under forest subsequently disappeared and could not be located. A second release, of 31 adults, in similar boulder conditions on the coast did not disperse and appears to have established (Parrish, 2008; B. Barr, pers. comm.; D. Towns, unpublished data). There have been similar differences in detectability in the Mercury Islands. Despite using release propagules (30) equal to or larger than those successful on Korapuki (Table 1) and consistent advice from one of us (D. Towns) over release site suitability, *O. alani* and *O. whitakeri* on Red Mercury and Kawhitu Islands appear to have dispersed beyond their respective release sites.

Table 2
Translocation success of tuatara and lizards mentioned in the text, including species for which genetic data have been obtained, using standardised criteria of [1]Miller et al. (2014), with additional data for tuatara on Titi in [2]Cree (2014); geckos on Mana Island ([3]Bell and Herbert, 2016); skinks on Hawea Island ([4]Thomas and Whitaker, 1995); and other locations from [5]Towns (unpublished), [6]Miller (2009), [7]Barr (pers. comm.) and [8]Parrish (2008); minimum number alive (MNA) is the sum of all known individuals in the population captured during the same field season (austral summer); *oviparous species, remainder viviparous; time of day active in parentheses as N (nocturnal); D (diurnal) or C (crepuscular); data for additional populations of tuatara are provided by Cree (2014).

Numerical success					Genetic effects
Stage	1: Survival of release propagule	2: Replacement through reproduction	3: Population growth	4: Population viable	
Sphenodon punctatus[1,2] (N)	Survival of release propagule 57% after year 1	First hatchling* found 11 years after release	None recorded	May require 100 years for replacement	Estimated optimum population size of 70 to retain maximum heterozygosity after 10 generations
Hoplodactylus duvaucelii[1,3] (N)	Only founders observed 10 years after release	First unmarked adult found after 11 years	Estimated 6-fold population increase at 15 years	Island-born animals comprise over 90% of captures, founders still present at 15 years; may require 50 years for replacement	No data
Oligosoma acrinasum[4] (D)	Survival of release propagule at least 35% after year 2	First juveniles observed at 6 months	Estimated 5-fold increase at 4 years	Island-born animals present in expanding population at 4 years, possibly supplemented by natural recolonisation	No data
O. alani[5] (N)	Survival of release propagule 64% up to year 8	First juvenile captured 5 years after release	MNA exceeded release propagule after 7 years; 14% of release propagule present after 16 years	Population colonising new sites; may require 30 years for replacement	Predicted loss of heterozygosity 10% over 10 generations
O. macgregori[5,7,8] (N)	No data	Likely replacement at 18 years but captures yet to exceed number released	None recorded		No data
O. oliveri[5] (N–C)	Only founders caught 4 years after release	First juvenile captured after 5 years, only locally-born adults at 17 years	Captures had not exceeded number released at 17 years		No data
O. suteri[3,5,6] (N)	Survival of release propagule 73% after year 1	First hatchling* captured 3.3 years after release	MNA exceeded release propagule after 6.3 years; 60% of release propagule still present at 7.3 years	Estimated 13-fold population increase after 14 years, replacement likely complete at 20 years	Average loss of heterozygosity 1% after 15 years
O. townsi[7,8] (N–C)	No data	No data	Number captured exceeded release propagule at 10 years		No data
O. whitakeri[5,6] (N)	Survival of release propagule 64% after year 1	First juvenile captured 4 years after release	MNA exceeded release propagule after 5 years; 11% of release propagule present after 16 years	Population colonising new sites, replacement complete at 21 years	Average loss of heterozygosity 8% after 20 years

Too few of either species have subsequently been located to assign the populations beyond Stage 2 of Miller et al. (2014).

4. Discussion

Ecological restoration through the removal of invasive mammals is a relatively new and rapidly growing initiative on islands (Keitt et al., 2011; Towns et al., 2016) and insular sites on the mainland (Innes and Saunders, 2011). Reintroductions to islands cleared of invasive mammals could potentially reduce extinction risks for many species. On New Zealand islands, pest eradication, relict population recovery and reintroductions could benefit tuatara and at least 29 species of lizards (Bellingham et al., 2010; our analyses). Reintroductions currently under way should benefit tuatara and at least 18 species of lizards, including 17 (20%) of those classified as threatened or at risk (Hitchmough et al., in press; Table 1). If potential benefits are to be are realised for reintroduced species of reptiles, it is necessary to understand 1) the optimal composition of release propagules (Armstrong and Seddon, 2007), 2) the most appropriate criteria for measuring success, and 3) the impediments to successful establishment.

At present, there are few empirical data to guide decisions about the optimal composition of propagules for reptile reintroductions. Artificially incubated eggs have contributed to 5 (39%) of tuatara releases, which have been either totally or largely based on animals raised in captivity. By comparison, only 2 (6%) of lizard reintroductions have involved captive reared animals.

On Korapuki Island, despite a starting population of only 14 (12 adults), *O. alani* now appears to have successfully established (Table 2). Also on Korapuki Island, particularly rapid population growth was recorded for *O. suteri* despite oviparous reproduction and potential egg mortality in nests (Towns and Ferreira, 2001). Our assessment indicates that *O. suteri* was the only species where twice as many females as males were released (Table 1). A sexually biased approach apparently also provided genetic advantages (see below).

In sum, propagule sizes and composition have varied. At present, the outcomes of all tuatara reintroductions and about 75% of lizard reintroductions have yet to be determined (see below), so the utility of particular reintroduction strategies remains unclear. A biased sex ratio to include twice as many (gravid) females as males shows promise at least for oviparous species. The rapid appearance of hatchling *Ameiva polops* two months after a population was reintroduced in the St Croix archipelago (US Virgin Islands) was attributed to inclusion of gravid females in the release propagule, although a female bias was not used (Fitzgerald et al., 2015).

The second issue that we identified involved defining criteria for successful reintroduction. Miller et al. (2014) suggested a staged approach with four standardised criteria for success. We located data for the outcomes of tuatara and 24% of all lizard reintroduction attempts (Table 2), which is a little more than the 15% obtained for all translocations of New Zealand herpetofauna by Miller et al. (2014). When these examples are assigned to the Miller et al. (2014) criteria, the gecko *H. duvaucelii* and at least three species of skinks are at Stage 4 (likely

viable in the long term) with few founders present. Three species are likely to have progressed beyond Stage 4 with replacement of founders (Wolf et al., 1996): *O. acrinasum*, *O. suteri* and *O. whitakeri*. None of these species is known to live for more than 20 years, each of them has shown population increases, and each of them was reintroduced at least 20 years ago. Others, such as *H. duvaucelii* and *O. alani* can show extreme longevity as adults. For example, *H. duvaucelii* in the wild likely reach at least 50 years of age (Bell and Herbert, 2016) and 14% of the release propogule of *O. alani* were still being caught after 16 years (Table 2). Tuatara will likely be slow to pass beyond Stage 2 (replacement through reproduction) because of their slow growth rates to maturity and extreme longevity of up to 91 years in the wild (N. Nelson unpublished data).

The third of our identified problems involved the impediments to successful reintroductions. Impediments revealed during our studies were at times numerous, complex and interactive (Fig. 2). For example, slow growth to maturity, low ARO and extreme longevity are likely characteristics of the rarer New Zealand species of reptiles (e.g. Cree, 1994; Towns, 1994). Whether there are additional behavioural impediments may not even be known. Regardless of biological issues, administrative conditions can influence project design, ease of monitoring reintroductions, and hence the ability to determine success. For example, Atiu or Middle Island (13 ha) is the only natural population of *O. whitakeri* that can withstand harvest for translocations, but activities on the island can damage the extremely dense seabird burrows. Reserve managers are understandably cautious about the frequency of visits to the island and the size of populations that can be removed (R. Chappell, pers. comm.), which can lead to propagule sizes that meet management objectives rather than biological ideals. We also identified cultural concerns about permanently marking animals for release. For *Dactylocnemis pacificus*, *O. macgregori* and *O. townsi* in the Marotiri Islands, the problem was overcome by only releasing adults. However, for these populations, detecting the long term outcome of the reintroduction has now become challenging: longevity of the founders cannot be determined nor can the point when founders cease to contribute to the population. Such species will thus become stuck at assessment Stage 3 (reported population growth).

Detectability may also depend on decisions about the site for release. Although such decisions may be based on experience of the researcher, detection after release depends on behaviour of the release propagule. Cryptic, species such as tuatara are extremely difficult to detect as young (Nelson et al., 2002), but difficulties can be increased by arboreal

Fig. 2. Conceptual model of factors that could influence the outcome of reptile reintroductions to islands based on long term studies in New Zealand. The model assumes that propagule size is influenced by all three core factors (ecological, administrative and genetic), but the intensity of effects and complexity of their links varies by species, site and available information.
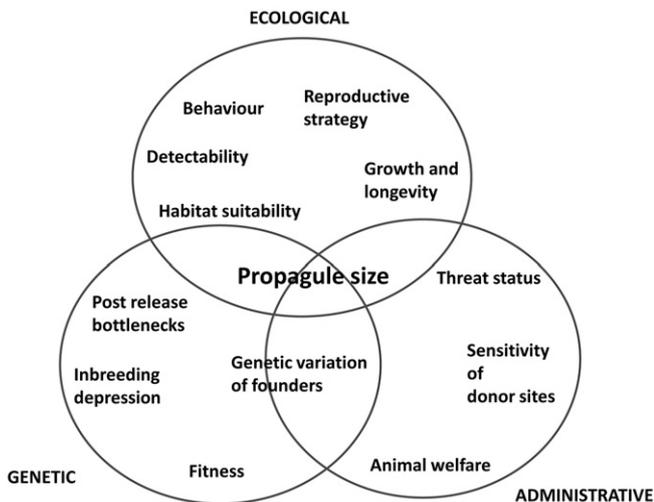
behaviour in geckos such as *H. duvaucelii* (Bell and Herbert, 2016) and the nocturnal and fossorial behaviour of tuatara and at least five of the species of skinks (Table 2). Furthermore, populations of the same species may respond in different ways to release. For example, whereas *O. alani* and *O. whitakeri* showed relatively high site fidelity on Korapuki Island, elsewhere in the Mercury archipelago the fate of reintroductions has been difficult to assess even though (at least for *O. whitakeri*) they originated from the same donor island.

In sum, the staged approach of Miller et al. (2014) to translocation outcomes provides an empirical chronosequence through stages of establishment. However, the rate at which reintroduced reptile populations pass along the sequence is likely to be heavily influenced by the reproductive biology, behaviour and detectability of each species. Furthermore, if the size and composition of release propagules is set by administrative or cultural considerations, there may be additional influences on detectability of released animals and the ability to identify founders (Fig. 2).

Up to this point, the effectiveness of reintroductions as a means of reducing extinction risk has rested on numerical criteria. However, conservation geneticists often warn that numerical "success" may hide latent genetic issues caused by bottlenecks (Traill et al., 2010; Weeks et al., 2011), especially when reintroduced populations are derived from small initial propagules (e.g. Jamieson, 2015). Unfortunately, there is little agreement over the threshold size at which populations might fail through genetic problems (Traill et al., 2010; Franklin et al., 2014) or even if genetic diversity is a good or a poor predictor of extinction risk (Jamieson and Allendorf, 2012). Nonetheless, having assumed that translocation reduces genetic diversity Weeks et al. (2011) suggested that pre-emptive mixing of populations should improve the evolutionary potential of newly established populations. This pre-emptive approach was used by Neuwald and Templeton (2013), who mixed four-five sources of the lizards *Crotaphytus collaris* for translocations in Missouri, USA. Similarly, in response to concerns about inbreeding within the Korapuki Island source for reintroductions of *H. duvaucelii* reinforcement releases used geckos from a second island (van Winkel et al., 2010; M. Barry pers comm.).

The earliest reintroductions of reptiles in New Zealand were in the late 1980s and early 1990s when mixing genetic stocks was viewed as a threat to genetic variation (e.g. Meffe, 1986) and an N_e of about 50 was viewed as sufficient to maintain genetic variability for translocated populations (e.g. Franklin et al., 2014). Although the size of release propagules in our study was reduced through management decisions, an N_e of 50 was obtained for *O. suteri* by releasing propagules biased to gravid females. When release propagules were based on random captures of *O. whitakeri* and *O. alani*, the loss of allelic diversity was higher than the population using female bias (Miller, 2009; Miller et al., 2011), but propagule size had little effect on the long-term numerical outcome. Both *O. alani* (n = 14) and *O. whitakeri* (n = 28) have established on Korapuki Island, appear to have lost similar proportions of allelic diversity as the result of a reintroduction bottleneck (Miller, 2009), but have achieved numerical viability although still without complete replacement for *O. alani* (Table 2). One possible reason for the relative success of *O. alani* is their high annual reproductive output and relatively quick post-release demographic recovery compared with *O. whitakeri*. These variable responses imply that the effects of propagule size may be species-specific and linked to reproductive strategies or other behavioural attributes such as male territoriality (Fig. 2). In the latter case, small numbers of males can sire much of the juvenile production, which is a strategy used by tuatara (Moore et al., 2008).

The conditions under which the genetic rescue should be applied remain unclear. Jamieson and Allendorf (2012) argue that steps such as population mixing are premature if the affected (reintroduced) populations continue to expand and if reduced fitness has not been demonstrated. Unfortunately, the links between genetic heterozygosity and fitness may be difficult to demonstrate for reptiles. When Miller et al. (2011) used sprint speed and dive duration as measures of fitness for

O. suteri, they found contradictory results presumably as a reflection of evolutionary advantages when individuals can respond in different ways to environmental variation (Miller et al., 2010). Other measures of fitness, such as survival (longevity) or breeding success (reproductive capacity) require decades to measure in long lived species, vary with body size, and are sensitive to population density (e.g. Cree, 2014). Furthermore, links between neutral genetic variation, using surrogates such as microsatellites, and functional effectiveness have not been clearly demonstrated (Jamieson and Allendorf, 2012). Modern genomic approaches (e.g. Stapley et al., 2010) should provide an opportunity to assess whether functional variation better matches fitness traits.

In sum, although we added a fifth criterion for translocation success – genetic effect – the only component that we have been able to provide is measured or predicted average loss of heterozygosity. Whether such a measure translates to fitness and hence might contribute to genetic criteria for population viability still remains unclear for reptiles and is also debated for non-reptilian groups.

A fourth question now becomes apparent: can reintroductions be designed as experiments that will inform debates about the viability of small populations (e.g. Sarrazin and Barbault, 1996; Armstrong and Seddon, 2007)? There do appear to be parallels between reintroduced populations and those heavily suppressed by habitat fragmentation or invasive species. Because the size and composition of reintroductions can be controlled, their outcomes might be applicable to wider ecological and genetic questions about the prospects for relict populations. For example, conflict over how to measure population viability using genetic information may stem in part from reliance on theoretical models in the absence of testable field examples (Jamieson and Allendorf, 2012). However, the incentives for reintroductions to islands are often to reduce extinction risks faced by rare species within the attendant constraints on propagule size. Such constraints limit the ability to randomise release sites and the capacity for contemporaneous replication. Despite these constraints, there are two key research topics that reintroductions could address. First, we identified a high proportion of tuatara reintroductions derived from eggs hatched in captivity. Although an expensive infrastructure may be needed, captive breeding would reduce pressure on host island populations for several species. In order to determine the cost efficiency of such an option, the outcomes of release from captive versus wild populations in a range of environments should be compared (e.g. Cree, 2014; Jarvie et al., 2015). These comparisons could include long term survival, susceptibility to disease and speed of colonisation.

Second, we should attempt to determine whether numerically successful reintroductions using constrained, single source propagules subsequently fail due to compromised genetic viability. Answers to this latter question will require that samples of reintroductions are allowed to run their course without further intervention—at least until the populations reach carrying capacity. We may then obtain some resolution to theoretical arguments about relationships between population size and evolutionary potential (Traill et al., 2010; Franklin et al., 2014). In the meantime, conservation managers need to be circumspect about claims of success for restoration projects involving long-lived reptiles and commit to long term studies of the reintroduced populations as they establish.

5. Conclusion

Global assessments of conservation status and knowledge needs for reptile conservation have identified the vulnerability of the faunas on archipelagos to invasive species (Böhm et al., 2013; Meiri and Chapple, 2016–this volume). One solution to these effects is eradication of invasive mammals and reintroduction through translocation of extirpated reptiles into their former range. New Zealand has a long history of reintroductions of reptiles to islands and those currently under way should reduce the extinction risk to tuatara and about 20% of the lizard fauna. Our assessment of the effectiveness of these reintroductions

indicates that 24% of projects involving lizards are now at, or close to achieving, criteria for numerical success, even though in one example <20 individuals were released. However, extreme longevity and low annual reproductive output mean that assessing numerical success for reintroductions may take decades for lizards and up to a century for tuatara. Nonetheless, careful studies of the ecological and genetic outcomes of these reintroductions are required if we are to understand the extent to which the traits demonstrated by more widely studied groups of vertebrates can be applied to reptiles.

References

Anderson, L., Cree, A., Towns, D.R., Nelson, N.J., 2015. Moving house: long-term dynamics of corticosterone secretion are unaltered in translocated populations of a rare reptile (the tuatara, *Sphenodon punctatus*). Conserv. Physiol. 3. http://dx.doi.org/10.1093/conphys/cov01 (in press).

Armstrong, D.P., Seddon, P.J., 2007. Directions in reintroduction biology. Trends Ecol. Evol. 23, 20–25.

Baling, M., Wedding, C., Barry, M., Ji, W., Brunton, D.H., 2010. Reintroduction of shore skinks to offshore islands in the Auckland Region, New Zealand. In: Soorae, P.S. (Ed.), Global Reintroduction Perspectives: 2010. IUCN/SSC Reintroduction Specialist Group, pp. 88–92.

Baling, M., van Winkel, D., Rixon (née Habgood), M., Ruffell, J., Ji, W., Ussher, G., 2013. A review of reptile research and conservation management on Tiritiri Matangi Island, New Zealand. N. Z. J. Ecol. 37, 272–281.

Bell, T., Herbert, S., 2016. Establishment of a self-sustaining population of a long-lived, slow-breeeding gecko (Diplodactylidae: Hoplodactylus duvaucelii) evident 15 years after translocation. J. Herpetol (in press).

Bellingham, P.J., Towns, D.R., Cameron, E.K., Davis, J.J., Wardle, D.A., Wilmshurst, J.M., Mulder, C.P.H., 2010. New Zealand island restoration: seabirds, predators, and the importance of history. N. Zeal. J. Ecol. 34, 115–136.

Böhm, M., Bollen, B., Baillie, J.E.M., et al., 2013. The conservation status of the world's reptiles. Biol. Conserv. 157, 372–385.

Cree, A., 1994. Low annual reproductive output in female reptiles from New Zealand. N. Z. J. Zool. 21, 351–372.

Cree, A., 2014. Tuatara: Biology and Conservation of a Venerable Survivor. Canterbury University Press, Christchurch.

Dodd, C.K., Siegel, R.A., 1991. Relocation, repatriation and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47, 336–350.

Fitzgerald, L.A., Treglia, M.L., Angeli, N., Hibbitts, T.J., Leavitt, D.J., Subalusky, A.L., Lundgren, I., Hillis-Starr, Z., 2015. Determinants of successful establishment and post-translocation dispersal of a new population of the critically endangered St. Croix ground lizard (*Ameiva polops*). Restor. Ecol. 23, 776–786.

Frankham, R., 2005. Genetics and extinction. Biol. Conserv. 126, 131–140.

Franklin, I.R., Allendorf, F.W., Jamieson, I.G., 2014. The 50/500 rule is still valid—reply to Frankham et al. Biol. Conserv. 176, 284–285.

Germano, J.M., Bishop, P.J., 2009. Suitability of amphibians and reptiles for translocation. Conserv. Biol. 23, 7–15.

Germano, J.M., Field, K.J., Griffiths, R.A., Culow, S., Foster, J., Harding, G., Swaisgood, R.R., 2015. Mitigation-driven translocations: are we moving wildlife in the right direction? Front. Ecol. Environ. 13, 100–105.

Hitchmough, R., Barr, B., Lettink, M., Monks, J., Reardon, J., Tocher, M., van Winkel, D., Rolfe, J., in press. Conservation Status of New Zealand Reptiles, 2015. Department of Conservation, Wellington.

Innes, J., Saunders, A., 2011. Eradicating multiple pests: an overview. In: Veitch, C.R., Clout, M.N., Towns, D.R. (Eds.), Island Invasives: Eradication and Management. IUCN, Gland, Switzerland, pp. 177–181.

IUCN/SSC, 2013. Guidelines for reintroductions and other conservation translocations. Version 1.0. Gland, Switzerland.

Jamieson, I.G., 2010. Founder effects, inbreeding, and loss of genetic diversity in four avian reintroduction programs. Conserv. Biol. 25, 115–123.

Jamieson, I.G., 2015. Significance of population genetics for managing small natural and reintroduced populations in New Zealand. N. Z. J. Ecol. 39, 1–18.

Jamieson, I.G., Allendorf, F.W., 2012. How does the 50/500 rule apply to MVPs? Trends Ecol. Evol. 27, 578–584.

Jarvie, S., Senior, A.M., Adolph, S.C., Seddon, P.J., Cree, A., 2015. Captive rearing affects growth but not survival in translocated juvenile tuatara. J. Zool. 297, 184–193.

Keitt, B., Campbell, K., Saunders, A., Clout, M., Wang, Y., Heinz, R., Newton, K., Tershy, B., 2011. The Global Islands invasive vertebrate eradication database: a tool to improve and facilitate restoration of island ecosystems. In: Veitch, C.R., Clout, M.N., Towns, D.R.

(Eds.), Island Invasives: Eradication and Management. IUCN, Gland, Switzerland, pp. 44–77.

Meffe, G.K., 1986. Conservation genetics and the management of endangered fishes. Fisheries 11, 14–23.

Meiri, S., Chapple, D., 2016. Biases in the current knowledge of threat status in lizards, and bridging the 'assessment gap'. Biol. Conserv 204, 6–15 (in this volume).

Miller, K.A., 2009. Founding Events and the Maintenance of Genetic Diversity in Reintroduced Populations. PhD thesis. Victoria University, Wellington.

Miller, H.C., Miller, K.A., Daugherty, C.H., 2008. Reduced MHC variation in a threatened tuatara species. Anim. Conserv. 11, 206–214.

Miller, K.A., Nelson, N.J., Smith, H.G., Moore, J.A., 2009. How do founder group size and reproductive skew affect genetic diversity in reintroduced populations? Mol. Ecol. 18, 3792–3802.

Miller, K.A., Hare, K.M., Nelson, N.J., 2010. Do alternate escape tactics provide a means of compensation for impaired performance ability? Biol. J. Linn. Soc. 99, 241–249.

Miller, K.A., Towns, D.R., Allendorf, F.W., Ritchie, P.A., Nelson, N.J., 2011. Genetic structure and individual performance following a recent founding event in a small lizard. Conserv. Genet. 12, 461–473.

Miller, K.A., Bell, T.P., Germano, J.M., 2014. Understanding publication bias in reintroduction biology: an assessment of translocations of New Zealand's herpetofauna. Conserv. Biol. 28, 1045–1056.

Miskelly, C., 2010. Mana Island Ecological Restoration Plan Review. Department of Conservation, Wellington 45pp.

Miskelly, C.M., Powlesland, R.G., 2013. Conservation translocations of New Zealand birds, 1863−2012. Notornis 60, 3–28.

Moore, J.A., Nelson, N.J., Keall, S.N., Daugherty, C.H., 2008. Implications of social dominance and multiple paternity for the genetic diversity of a captive-bred reptile population (tuatara). Conserv. Genet. 9, 1243–1251.

Nelson, N.J., Keall, S.N., Brown, D., Daugherty, C.H., 2002. Establishing a new wild population of tuatara (*Sphenodon punctatus*). Conserv. Biol. 16, 887–894.

Nelson, N., Keall, S., Gaze, P., Daugherty, C., 2008. Reintroduction of tuatara as part of an ecological restoration project on Wakatere-papanui Island, Marlborough Sounds, New Zealand. In: Soorae, P.S. (Ed.), Global Reintroduction PerspectivesIUCN/SSC Reintroduction Specialist Group. Environment Agency Abu Dhabi and Denver Zoological Foundation, pp. 58–61.

Nelson, N.J., Hitchmough, R., Monks, J.M., 2014. New Zealand reptiles and their conservation. In: Stow, A., Maclean, N., Holwell, G. (Eds.), Austral Ark: the State of Wildlife in Australia and New Zealand. Cambridge University Press, pp. 382–404.

Neuwald, J.L., Templeton, A.R., 2013. Genetic restoration in the eastern collared lizard under prescribed woodland burning. Mol. Ecol. 22, 3666–3679.

Parrish, R., 2008. Re-introduction of skink and gecko species to Marotere Islands, Northland, New Zealand. In: Soorae, P.S. (Ed.), Global Re-introduction PerspectivesIUCN/SSC Reintroduction Specialist Group. Environment Agency Abu Dhabi and Denver Zoological Foundation, pp. 62–65.

Sarrazin, F., Barbault, R., 1996. Reintroduction: challenges and lessons for basic ecology. Trends Ecol. Evol. 11, 474–478.

Saunders, A., 1995. Translocations in New Zealand: an overview. In: Serena, M. (Ed.), Re-introduction Biology of Australian and New Zealand Fauna. Surrey Beatty and Sons, Chipping Norton, Australia, pp. 43–46.

Shaffer, M., 1981. Minimum population sizes for species conservation. Bioscience 31, 131–134.

Sherley, G.H., Stringer, I.A.N., Parrish, G.R., 2010. Summary of native bat, reptile, amphibian and terrestrial invertebrate translocations in New Zealand. Science for Conservation 303. Wellington, Department of Conservation.

Stapley, J., Reger, J., Feulner, P.G.D., Smadga, C., Galindo, J., Ekblom, R., Bennison, C., Ball., A.D., Beckerman, A.P., Slate, J., 2010. Adaptation genomics: the next generation. Trends Ecol. Evol. 25, 705–712.

Thomas, B.W., Whitaker, A.H., 1995. Translocation of the Fiordland skink *Leiolopisma acrinasum* to Hawea Island, Breaksea Sound, Fiordland, New Zealand. In: Serena, M. (Ed.), Reintroduction Biology of Australian and New Zealand Fauna. Surrey Beatty and Sons, Chipping Norton, Australia, pp. 91–95.

Towns, D.R., 1975. Ecology of the black shore skink, *Leiolopisma suteri* (Lacertilia: Scincidae), in Boulder beach habitats. N. Z. J. Zool. 2, 409–423.

Towns, D.R., 1994. The role of ecological restoration in the conservation of Whitaker's skink (*Cyclodina whitakeri*), a rare New Zealand lizard (Lacertilia: Scincidae). N. Z. J. Zool. 21, 457–471.

Towns, D.R., 2002. Korapuki Island as a case study for restoration of insular ecosystems in New Zealand. J. Biogeogr. 29, 593–608.

Towns, D.R., Atkinson, I.A.E., 2004. Restoration Plan for Korapuki Island (Mercury Islands), New Zealand 2004–2024. Department of Conservation, Wellington.

Towns, D.R., Ferreira, S.M., 2001. Conservation of New Zealand lizards (Lacertilia: Scincidae) by translocation of small populations. Biol. Conserv. 98, 211–222.

Towns, D.R., West, C.J., Broome, K.G., 2013. Purposes, outcomes and challenges of eradicating invasive mammals from New Zealand islands: an historical perspective. Wildlife Res. 40, 94–107.

Towns, D.R., Borrelle, S.B., Thoresen, J., Buxton, R.T., Evans, A., 2016. Mercury Islands and their role in understanding seabird island restoration. N. Z. J. Ecol. 40, 235–249.

Traill, L.W., Brook, B.W., Frankham, R.R., Bradshaw, C.J.A., 2010. Pragmatic population viability targets in a rapidly changing world. Biol. Conserv. 143, 28–34.

Van Winkel, D., Baling, M., Barry, M., Ji, W., Brunton, D.H., 2010. Translocation of Duvaucel's geckos to Tiritiri Matangi and Motuora Islands, Hauraki Gulf, as part of island ecological restoration initiatives. In: Soorae, P.S. (Ed.), Global Reintroduction Perspectives: 2010. IUCN/SSC Reintroduction Specialist Group, pp. 113–117.

Weeks, A.R., Sgro, C.M., Young, A.G., Frankham, R., Mitchell, N.J., Miller, K.A., Byrne, M., Coates, D.J., Eldridge, M.D.A., Sunnucks, P., Breed, M.F., James, E.A., Hoffman, A.A., 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evol. Appl. 4, 709–725.

Wolf, C.M., Griffith, B., Reed, C., Temple, S.A., 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conserv. Biol. 10, 1142–1154.