Predictors of translocation success of captive-reared lizards: implications for their captive management

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Abstract

Islands are biodiversity hotspots, but their native inhabitants are vulnerable to predation from exotic predators. Conservation of island endemics has often involved translocating captive-reared populations to predator-free refugia. However, the long-term success of these translocations has rarely been assessed. We investigated the traits that maximize post-translocation survival in a cohort of captive-reared Suter's skinks *Oligosoma suteri* and compared traits normally associated with survival and persistence of lizards (body condition, speed and overall size) to that of wild-born skinks 6 years after release onto a predator-free island in the north-east of New Zealand. Our models showed that larger lizards, and lizards with lower body condition, had improved survival. While sprint speed of captive-reared lizards did not differ significantly to that of wild skinks, diving ability of captive-reared skinks was poor, with only female captive-reared lizards diving during trials. Our results indicate that the traits associated with higher survival after release are not necessarily obvious and may be influenced by adaptation to captive conditions. Long-term monitoring post-translocation is therefore vital to determine the success of the translocation.

Introduction

Globally, islands represent important biodiversity hotspots (Myers *et al.*, 2000). They support a large number of endemic taxa, and often contain species or lineages that are predominantly, or entirely, represented on islands (Cowie & Holland, 2003; Whittaker & Fernández-Palacios, 2007). Thus, when adjusted for area, islands collectively support a disproportionate number of the world's species (Myers *et al.*, 2000; Whittaker & Fernández-Palacios, 2007). Insularity has favoured selection for low reproductive output and high longevity (Cree, 2005; Whittaker & Fernández-Palacios, 2007; Covas, 2012), while release from predation pressure on islands has resulted in a loss or modification of anti-predator behaviours (Blumstein & Daniel, 2005; Whittaker & Fernández-Palacios, 2007). Combined with their restricted geographic ranges, these island-specific behavioural traits mean that island species are especially vulnerable to anthropogenic threats (IUCN, 2018).

A key threat to island fauna is the introduction of exotic species, which compete with island biota, alter habitat and prey upon native species (Towns *et al.*, 2006; Doherty *et al.*, 2016). Introduced vertebrate predators, especially rodents, pose a particular threat. These have established on numerous offshore islands where they prey upon naïve island fauna, reducing reproductive success and recruitment and displacing and suppressing island populations (reviewed in Towns *et al.*, 2006). The consequences for island endemics are devastating (Towns *et al.*, 2006; Stolzenburg, 2011), with introduced predators implicated in a considerable number of extinctions and declines. Indeed, a disproportionate number of island species have been lost to extinction (reviewed in Doherty *et al.*, 2016). Accordingly, islands are also hotspots of extinction (Myers *et al.*, 2000; Whittaker & Fernández-Palacios, 2007).

New Zealand is a world leader in conservation management of species threatened by introduced predators (Armstrong & McClean, 1995; Romijn & Hartley, 2016; Towns *et al.*, 2016a). Management has focused on eradicating mammalian predators from islands before translocating native species to these island refugia, either to reinforce existing

populations or to found new populations (Towns et al., 2016a,b, Hitchmough *et al.*, 2016a). Translocated individuals may be bred in captivity (Seddon et al., 2007; Maran *et al.*, 2009) and are often 'head-started' prior to their release (Connolly & Cree, 2008; Jarvie *et al.*, 2015). While the success of wildlife translocations has traditionally been difficult to quantify, Miller *et al.* (2014) proposed a staged approach to define translocation success using four standardized criteria: survival and growth of individuals, evidence of reproduction, population growth and population viability. Based on this approach, a translocation is considered a success when released populations meet or exceed one of the four stages during monitoring (Miller *et al.*, 2014).

Miller *et al.*'s (2014) standardized criteria for translocation success were developed using data from the New Zealand herpetofauna, of which lizards are the major components. New Zealand has a diverse, endemic lizard fauna comprising ~104 species (61 Eugongylinae skinks, 43 Diplodactylidae geckos; van Winkel *et al.*, 2018; Hitchmough, 2016). However, 83% of species are regarded as threatened or at risk, with introduced mammalian predators representing the primary threat (Tingley et al., 2013; Hitchmough *et al.*, 2016a; Towns *et al.*, 2016b). Consequently, many New Zealand lizard species have declined on the main islands (North Island, South Island) and primarily persist on smaller, offshore islands (Chapple & Hitchmough, 2016; Towns *et al.*, 2016b).

Conservation attempts have involved translocating lizards to offshore islands or mainland refugia, and in New Zealand, captive management is increasingly being used to found populations for translocation to new sites. However, the success of such translocations has generally been undetermined or assessed over relatively short timescales; longer term monitoring (>4 years) is required to direct future translocation efforts (Romijn & Hartley, 2016; Towns *et al.*, 2016a). We investigated the success of a translocation of a population of captive-reared Suter's skinks on an offshore island of New Zealand as well as the factors likely to predict success. To this end, we used as our case study a cohort of captive-reared Suter's skinks (*Oligosoma suteri*) that were hatched from eggs of females collected from Green Island off the north-east coast of New Zealand and head-started to 18 months of age before being translocated to nearby Korupuki Island in 2001. This represents the only translocated population of captive-reared lizards in New Zealand for which long-term data are available. Locomotor performance of recaptured individuals from this population was compared to wild individuals captured from Korapuki Island in 2006 (Miller et al., 2010). The wild population is the result of a successful translocation of 10 male and 20 gravid female founders successfully translocated from Green Island to Korapuki Island in 1992 (see Towns & Ferreira, 2001 for details of this translocation). The translocation sites were similar in appearance, with similar sized rocks. However, the Towns & Ferreira (2001) translocation of adults to the northern beach was north facing, and likely received more sunshine hours, and had a gentle slope up to the forest; the second translocation of juveniles was to a southern facing beach with a cliff face up to the forest.

The nocturnal Suter's skink is the only oviparous lizard species endemic to New Zealand (Cree & Hare, 2005). It is a medium-sized (maximum snout-vent length (SVL) of *c.* 108 mm, Hardy, 1977) skink that is restricted to rocky beaches of northern New Zealand (Hare *et al.*, 2008a; Chapple & Hitchmough, 2017), presumably due to cooler temperatures at more southerly latitudes (Hare *et al.*, 2004). It is vulnerable to introduced predators (Towns *et al.*, 2003) and has experienced significant range reductions in recent years, with the species now largely limited to offshore islands (Towns & Ferreira, 2001; Towns *et al.*, 2016b). Individuals are long-lived, reaching at least 12 y in the wild (Towns & Ferreira, 2001), and typically deposit their first clutch at ~33 months after hatching (Towns, 1975). The breeding season is broadly mid-Spring to Summer, with ovulation occurring in October–November and oviposition in late December–early January (Towns, 1975).

Hare *et al.* (2012) reported the short-term (~12–18 months pre-release) outcomes of captive rearing prior to release of Suter's skinks to Korupuki Island. Here we report on the longer-term outcomes (~5.5 years) of the translocated Suter's skink population to assess the success of this translocation as per Miller *et al.* (2014), and explore the factors that influence translocation success. Specifically, we examine:

1 the key factors that can be measured prior to release that impact survival of captive-reared lizards in the wild (sex, body condition, mass at hatching and at 12 months, and sprint speed at 4 months, selected because these are commonly measured during translocation programmes and are therefore relevant to other programmes attempting to gauge translocation success), and

2 how locomotor performance of translocated captive-reared adults compares to wild individuals post-release.

We expected that over the timeframe of the study, evidence of survival, growth and reproduction (Miller *et al.*, 2014) would be detected if this translocation has been successful, but longer term data would be necessary to evaluate whether this population has met Miller *et al.*'s (2014) remaining criteria for translocation success (population growth and viability). Our study will help determine whether captive rearing programmes represent a viable conservation technique for Suter's skinks, and will facilitate consideration of the potential impacts of captive rearing on the likelihood of translocation success in lizards. In addition to furthering our understanding of what influences translocation success, much of the information revealed in this study will assist managers to predict the potential quality of captive-reared founders (i.e. individuals that are likely to produce successful translocation outcomes). This will enable the most suitable candidates for release into the wild to be identified.

Materials and methods

Egg collection and incubation

Details of egg collection and incubation are described in full in Hare et al. (2002), and in Hare *et al.* (2004, 2008b).

Briefly, eggs were collected from 58 female Suter's skinks, sourced from Green Island, Mercury Island group, New Zealand (36°38'S, 175°51'E, 1–2 m a.s.l.) in Summer, 1999. The eggs were randomly assigned to one of three incubation temperatures (18°C, 22°C and 26°C) and one of two water potentials (−120 and −270 kPa). Each clutch (two to five eggs per clutch, Hare *et al.*, 2002) was (where possible) represented at all three temperatures, but at only one water potential per temperature. Water potential of the vermiculite incubation medium had no influence on any variables by 12 months of age (Hare *et al.*, 2004; 2008b) and is not considered further.

Juvenile maintenance

Immediately after hatching, we attempted to identify sex, and individuals were weighed (±1 mg), measured (SVL and tail length, ±0.5 mm) and permanently marked by toe clipping. Skinks were initially housed in groups of three under the same conditions that gravid females were provided, in transparent boxes (215 × 330 × 110 mm, 7 L) with a lid containing 1 mm^2 wire mesh (165 × 120 mm) for ventilation. At least 20 mm of moist, non-fertilized potting mix was used as the substrate and pieces of bark were provided for shelter. A heat strip at one end of each box provided a temperature range of 14–30°C. At 5–8 months of age, juveniles were re-sorted by size into groups of 6–12 in metal enclosures (700 × 580 × 350 mm) with 1 mm^2 mesh lids. The metal enclosures were lined with 50 mm of sand, with driftwood, dried seaweed and small stones for shelter. Juveniles continued to be periodically re-sorted by size.

Juveniles were given free access to water and fed *ad libitum* with live food items and fish-based cat food. Live food was regularly supplemented with calcium powder and vitamin drops (Avi-Cal^{TM}; calcium borogluconate 200 g/L, cholecalciferol (Vitamin D$_3$) 12 500 IU/L and magnesium sulphate 5 g/L). Day/night was simulated using UV bulbs (Duro-test® True-lite® power twist fluorescent tubes) on a 12L:12D light cycle.

Release, monitoring, survival and reproduction post-release

Of the 136 hatchlings, 94 (69.1%) survived the 18 months until release in early October 2001 (Hare *et al.*, 2004; this study). These were released *en masse* on a south-facing beach (hereafter Release Beach) on Korapuki Island, Mercury Island group, New Zealand (36°39'S, 175°50'E 36, 1-2 m a.s.l), ~1.75 km from the source location of Green Island. The release site is separated from other beaches on the island by steep cliffs; while Suter's skinks have previously been translocated to Korapuki Island (Towns & Ferreira, 2001), those skinks in previous translocations were released on a north-west facing beach ~200 m (coastal distance) from Release Beach. At that time there was no evidence of existing Suter's skink individuals occupying Release Beach (Towns unpubl. data). Both translocated

populations of lizards were exposed to a suite of native predators, and for New Zealand lizards it included birds, bigger reptiles and invertebrates (Hare *et al.*, 2016).

We conducted a mark–recapture exercise in 2005 and 2007, approximately 4–6 years after release. Due to the cost and permits required to undertake research on protected islands in New Zealand, the timing and effort involved in the monitoring trips was opportunistic, and part of much larger scientific events. In 2006, we measured the locomotor performance of recaptured individuals, and were therefore unable to do a mark–recapture study as individuals were captured for the experiments. For mark–recapture studies, the site was monitored over 5 days on 18–22 November 2005 and 28 February–4 March 2007. Five pitfall trapping sites were established: three on Release Beach, and one each on beaches to the east and west of Release Beach (to determine if skinks were expanding around the island). On Release Beach, trapping sites were located: (A) at the initial release site, (B) 20 m west of the initial release site and (C) 40 m west of the initial release site. At Sites A and B, pitfall traps were set at 2-m intervals in three lines of five, positioned from the storm line (bottom of the cliff face) to the high-tide mark. At Site C and the western beach, we placed two sets of four traps midway between the storm line and the high-tide mark at 2-m intervals. At the eastern beach, we used a permanent lizard monitoring transect of 20 traps in five stations, each 20 m apart along the storm line with four traps set on the corners of each 2 × 2 m station. All traps comprised 4l plastic paint pails that were provided with cover and baited daily with canned cat food. Traps close to the high-tide mark were covered with galvanized netting to stop entry by large crabs, which are known to prey upon trapped lizards (Hare *et al.*, 2016) and indeed even wild-ranging lizards (Bell & Bauer, 2008). We placed large flat rocks upon the traps, with gaps beneath, to prevent captured lizards from overheating in the sun. On the south-eastern beach, each of the four traps at each station was baited with either fish- or meat-based cat food, canned pear, or left unbaited. Except for traps placed on the south-eastern beach, all traps were set for *c.* 12 h, and checked in the early morning and late evening for 5 days. The south-eastern beach traps were checked at intervals of 48 h and set three times over 6 days.

Sex, mass (±0.5 g), SVL (±0.5 mm) and for females, gravidity status were recorded for recaptured individuals during each year of trapping. Sex was determined by eversion of the hemipenes in males. Gravidity status and an estimate of clutch size were obtained via abdominal palpation by a trained expert (KMH).

Locomotor performance

We used sprint speed and dive duration as measures of locomotor performance post-release in 2006. The methods used to measure these locomotor performance traits in other *O. suteri* individuals are described in detail in Miller *et al.* (2010). Briefly, both speed and diving trials were conducted under natural photoperiods (14:10 light:dark cycle, with sunrise at ~0600 h) and at ambient air temperatures averaging 17.5 ± 0.05°C. Three trials were conducted within 1 day for

both performance measures, and all individuals were at least 2 days post-absorptive. Dive trials were conducted after completion of sprint trials, with a minimum of 120 min rest between trials of the two performance measures.

Sprint speed was measured between 0930 h and 1230 h using a field portable timer (Huey *et al.*, 1981). The order of individuals was randomized over the three trials, but in all cases, individuals were given at least 15 min rest between trials. A plastic racetrack (1.5 × 0.8 m), with five paired infrared lights (0.25 m apart and 4 mm high) over 1 m, was used to test sprint speed. The lights transmitted and received an infrared beam horizontally across the track, and the interruption of each successive infrared beam stopped its paired timer. The fastest speed over 0.25 m was used in analyses since burst speed is likely to be a more ecologically relevant measure for species that live on rocky shores where long sprints are not necessary to reach cover. To encourage sprinting, we gently touched the tails of lizards with a paintbrush. We also recorded the number of pauses, scored when an individual ran forwards after its tail was touched before stopping and requiring another touch to continue, over 1 m. Performance in captive-reared individuals was compared with that of wild-born individuals, captured from the northern release beach; these data were published in Miller *et al.* (2010).

Voluntary diving trials were undertaken in an artificial rock pool between 1530 h and 1930 h. The order of individuals was randomized over the three trials and animals were given at least 60 min rest between each dive trial. The artificial rock pool comprised a darkened round plastic bin (base 340 mm diameter; 20 L to fill line) filled with rocks (in a centre spire with one emergent rock), seaweed and intertidal seawater (mean temperature 16.7 ± 0.07°C; modified from Hare & Miller, 2009). Skinks were placed on the emergent rock facing away from the researcher and diving was encouraged by tapping on the tail. Some skinks did not dive, and instead swam about on the surface of the water; if these animals did not dive after 10 sec, they were removed. If an animal dived, we recorded dive duration (i.e. the time between submergence and emergence) using a manual stopwatch (accurate to 1 sec). Dive duration of captive-reared skinks was compared to that of wild-born individuals, using data from Miller *et al.* (2010).

Statistical analyses

In order to determine the factors that influenced long-term survival of captive-reared Suter's skinks, we fitted a Bayesian Cormack-Jolly-Seiber (CJS) survival model (hereafter, full model). To account for differences in trap days, detection probability was included as a fixed effect with a random effect of year (eq. 1).

$$\text{logit(observation)} \sim 1 + \text{random}_{\text{effect}}(\text{year of survey}) \quad ((1))$$

Survival probability was modelled as a function of sex, mass at 12 months, mass at hatching and body condition (eq. 2). In order to account for the 5-year gap between release and the first trapping period, year since release was treated as a two level factor (i.e. Year 1 and the following years) within the survival component of the model (eq. 2). We calculated body condition according to whether individuals were heavier or lighter than predicted for their length based on the residuals from the estimated mass using log/log allometric equations.

$$\text{logit(survival)} \sim \text{mass}_{12\text{months}} + \text{mass}_{\text{hatching}} \\ + \text{ body cond}_{12\text{months}} + \text{factor(yr since release)} \quad (2)$$

The influence of sprint speed at 4 months on survival post-release (Hare *et al*, 2008b) was incorporated into a separate model, following the same structure, using a reduced dataset to include only those individuals that were run in sprint speed trials upon recapture (hereafter, reduced model). Snout–vent length (SVL) was omitted from all models due to its high correlation with mass. Analyses were carried out using JAGS (Plummer, 2003) through R (R Core Team, 2017) using the r2hags package (Su & Yajima, 2015).

Sprint speeds of captive-reared individuals were compared to those of 63 wild-caught individuals, all males, from Miller *et al.* (2010) using a linear regression that modelled sprint speed against the interaction of snout–vent-length and type (captive-reared or wild-caught) (eq. 3). To enable a fair comparison with adult wild-caught animals, sprint speeds of captive reared individuals were those measured upon recapture as adults and not the juvenile sprint speed used in the survival analysis.

$$\text{sprint speed} \sim \text{snout} - \text{vent} - \text{length} * \text{factor(type)} \quad (3)$$

Results

Survival, size and reproduction

In total, 21 captive-reared individuals were recaptured over the 3 years, with an additional three unmarked individuals captured in 2006 and 2007 (SVL range = 55–80 mm). Of the marked individuals, 17 captures of 10 individuals were made in 2005, 10 individuals were trapped in 2006 and 25 captures of 17 individuals were recorded in 2007. Recaptured individuals were incubated at either 22°C ($n = 12$) or 26°C ($n = 9$); no individuals incubated at 18°C were recaptured. All recaptures were from Release Beach, and most were from the original release site (transect A; 78% of captures), with some from transect B (20 m south of the release site; 22% of captures), and none from transect C (40 m south of the release site). No Suter's skinks were captured from beaches directly north or south of Release Beach.

Size of individuals increased during the course of the 7-year study, with growth rate averaging 7.1 mm per year. At hatching, mean SVL and mass of the 21 individuals was 34.9 ± 0.16 mm and 0.77 ± 0.01 g, respectively, and by November 2005, all recaptured individuals had attained size-based maturity (Towns, 1975, Table 1). The average size and weight of individuals continued to increase during the course of the study (Table 1).

In November 2005, three of five females were gravid with 1–2 eggs, and in November 2006, all five females captured were gravid with 1–3 eggs. Two females were captured in both 2005 and 2006, and of these, one was gravid with one egg in both years, and the other was only gravid in 2006.

Factors influencing survival probability

The full model indicated strong support (at the 95% confidence level) for a positive influence of mass at 12 months on lizard survival, with larger lizards experiencing greater survival, but no influence of mass at hatching (Table 2, Fig. 1). In contrast, body condition negatively impacted survival. This suggests that individuals who are heavier, but lighter than predicted for their length, are more likely to survive (Fig. 2). These findings were replicated in the reduced model, which also did not show support (at the 95% confidence level) for a relationship between sprint speed and survival (Table 3).

Locomotor performance comparisons

Gravidity in female skinks has been shown to affect sprint speed (Shine, 1980). Unfortunately, we only had sprint speed information for gravid captive-reared females (present study) and non-gravid, wild females, caught from the northern
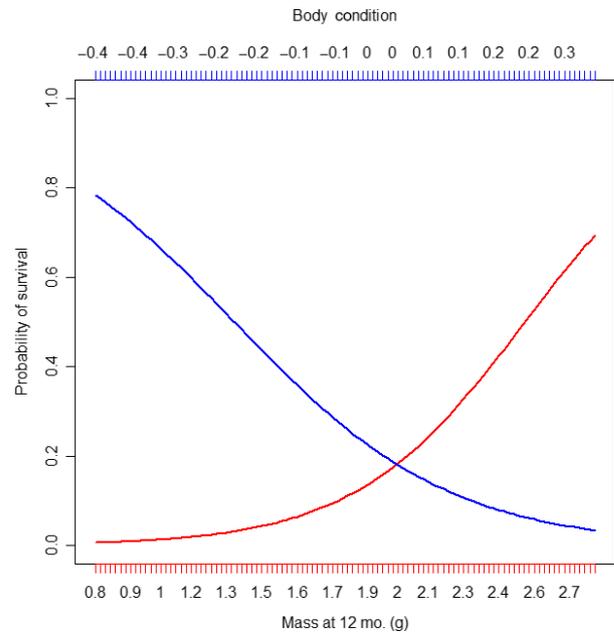

Figure 1 Estimated probability of survival from year one showing individual influential responses for body condition (blue) and mass (red) in Suter's skinks (*Oligosoma suteri*) [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]
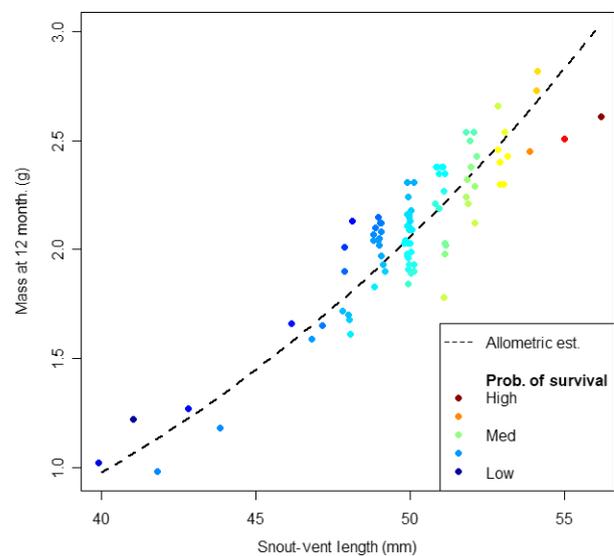
Table 1. Mean snout–vent length (SVL) and weight of Suter's skinks *Oligosoma suteri* throughout the course of the study. Values in parentheses represent range

Date (age)	SVL (mm)	Mass (g)
Feb–Jun 2000 (hatching)	34.9 ± 0.16 (28-38)	0.76 ± 0.01 (0.33–0.92)
Feb–Jun 2001 (12 months)	49.9 ± 0.3 (40–56)	2.07 ± 0.04 (0.77–2.82
November 2005 (<6 years)	80.56 ± 0.85 (75–84)	10.17 ± 0.41 (8.5–13)
November 2006 (<7 years)	83.4 ± 0.48 (82–87)	10.58 ± 0.19 (9.75–11.8)
March 2007 (7 years)	84.81 ± 0.59 (81–89)	10.81 ± 0.38 (8.25–12.8)

Table 2. Results of Bayesian BJS survival model for the survival of captive raised skinks released into the wild. Italicized and underlined values indicate those where a strong level of support (95% CIs do not cross 0) for their influence on survival were detected

	Mean	SE	2.50%	97.50%
Mass (12 mo)	*1.056*	*0.486*	*0.248*	*2.132*
Mass (0 mo)	0.013	0.332	−0.590	0.707
Condition	*−0.945*	*0.489*	*−2.074*	*−0.157*
Year(1)	*−1.313*	*0.320*	*−1.958*	*−0.711*
Years(2:4)	*82.229*	*58.697*	*7.444*	*222.100*
Intercept (obs. probability)	*−1.402*	*0.562*	*−2.160*	*−0.635*
Sigma	*0.467*	*0.785*	*0.012*	*2.096*

Figure 2 Observed (points) and estimated (dashed line) mass of Suter's skinks (*Oligosoma suteri*) by snout–vent length. Estimated line indicates allometric equation (log[mass] ~ log[length]) generated from the observed data. Point colour indicates the estimated probability of survival based on fitted survival model. Note: *X*-axis values have a precision s mm but have been 'jittered' to improve visibility [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

Table 3. Results of Bayesian BJS survival model, on reduced dataset including only those individuals where sprint speed informations were detected, for the survival of captive raised skinks released into the wild. Italicized and underlined values indicate those where a strong level of support (95% CIs do not cross 0) for their influence on survival were detected

	Mean	SE	2.50%	97.50%
Mass (12 mo)	_1.805_	_0.702_	_0.621_	_3.402_
Mass (0 mo)	0.005	0.533	−1.053	1.107
Condition	_−1.617_	_0.597_	_−2.883_	_−0.549_
Sprint Speed	−0.520	0.528	−1.656	0.441
Year (1)	_−1.867_	_0.438_	_−2.793_	_−1.085_
Years (2:4)	_83.890_	_60.963_	_7.400_	_229.463_
Intercept (obs. probability)	_−1.369_	_0.450_	_−2.190_	_−0.551_
Sigma	_0.455_	_0.656_	_0.011_	_2.054_

Release beach (Miller *et al.*, 2010). Therefore, to avoid the confounding effect of reproductive status, we did not compare speed in these. Hence, only males were included in statistical comparisons of sprint speed. These comparisons indicated no significant differences in maximum sprint speeds between captive-reared and wild-born males ($P > 0.05$ for all covariates), with average sprint speeds of 1.05 ± 0.06 m/s (range 0.89–1.21) and 1.12 ± 0.03 (range 0.79–2.21) attained by captive-reared and wild-caught male, respectively. Captive-reared (gravid) and wild-caught (non-gravid) females achieved mean speeds of 0.74 ± 0.13 (range 0.45–1.05) and 1.05 (0.87–1.27) respectively.

Captive-reared lizards rarely dived; of the 10 captive-reared individuals (five males and five gravid females) used in dive trials, only four (40%) dived in at least one trial. Two skinks (20%) dived in all three trials and six (60%) did not dive in any of the trials. Instead, for the majority of dive trials, lizards swam about the water surface. All individuals who dived were female, with dive durations averaging 124 ± 35.5 s (range 22.2–185.8 s).

Discussion

Larger, leaner lizards have a higher probability of survival following translocation

Unlike previous studies on survival of this species, which investigated the factors influencing survival in captivity (e.g. Hare *et al.*, 2004, 2008b), our study presents novel data on long-term post-release outcomes for captive-reared Suter's skinks. These indicate that the best predictors of survival of Suter's skinks post-translocation are size and body condition; both larger lizards and lizards with lower body condition at 12 months experienced greater survival. The magnitude of the size difference between skinks is large enough to be biologically significant, with a 16-mm and 2.05 g difference in SVL and weight, respectively, between the smallest and largest individuals about 12 months old. These results have implications for the increasing use of captive management

for threatened species and suggest that larger, leaner lizards should be prioritized for translocations.

Higher survival might be expected in larger lizards for several reasons. Firstly, bigger individuals typically have larger heads, with positive follow-on effects on bite force (Herrel *et al.*, 1999; Herrel et al., 2001; Verwaijen et al., 2002), prey handling efficiency and the ability to eat bigger and harder-bodied prey (Verwaijen *et al.*, 2002). In addition, larger lizards may have fewer predators than their smaller counterparts, with some predators preferentially selecting, or limited to, smaller prey individuals (e.g. Hasegawa, 1990; Webb & Shine, 1993). Finally, greater size confers a competitive advantage, with larger-bodied individuals more likely to win agonistic interactions (Tokarz, 1985; Cooper & Vitt, 1987; Sacchi *et al.*, 2009), thereby maximizing their ability to secure key resources, such as territories (Sacchi *et al.*, 2009), favourable perching sites (Tokarz, 1985), food (Stamps, 1977) and optimal basking and refuge sites (Carothers, 1981).

Large size also has reproductive benefits. Body size in skinks has a positive relationship with clutch and litter size (Cree & Hare, 2005; Chapple, 2006, 1994; Chapple *et al.*, 2014), and Suter's skinks are no exception, with females of a greater SVL producing significantly more eggs (Hare *et al.*, 2002). Thus, not only did larger individuals experience higher survivorship, but they likely also have greater reproductive output. This could potentially increase the overall likelihood of translocation success (Towns *et al.*, 2016a).

The reduced survival of skinks with higher body condition seems counter-intuitive. Lipid reserves of lizards provide an energy store during lean periods (Avery, 1970; Derickson, 1976), and support reproduction, growth and maintenance (Derickson, 1976), so it is logical that heavier translocated lizards, with their presumably greater fat reserves to draw on, should have improved survival. So why would Suter's skinks experience the opposite following translocation? The answer may simply be that they are overly acclimated to captive conditions. These can influence phenotype, including social and anti-predator behaviour (Snyder *et al.*, 1996; Connolly & Cree, 2008), and produce inactive, overweight individuals (Connolly & Cree, 2008) that are less adept at capturing prey in the wild; when the fat reserves of these individuals are depleted, their survival is compromised. In contrast, Hare *et al.* (2012) found no influence of body condition index or size on survival post-release in captive-reared Otago skinks (*O. otagense*), potentially a function of differences in sample size, species and/or the amount of time post-release over which monitoring was conducted. Nonetheless, our results suggest that captive management can result in selection for unfavourable traits in lizards.

It is also possible that underlying factors that affect phenotype, such as the rearing environment and maternal effects, are driving survival post-release. For example, maternal effects, which influence traits such as body size and condition (e.g. Shine & Harlow, 1993; Wapstra, 2000), may be the causal drivers behind the relationships observed here rather than body size and condition *per se*. Regardless of the proximate mechanism, it is reasonable to use phenotypic

traits, which can be easily and routinely measured by captive managers, as predictors of survival since phenotype is an expression of these underlying factors.

Lizards that were incubated at 18°C were not recaptured 4 or more years after the translocation, supporting Hare *et al.*'s (2004) suggestion that individuals incubated at this temperature would not survive to maturity. Such low survival rates may be due to the smaller body sizes reached by these individuals at 12 months (Hare *et al.*, 2004) or a consequence of the increased rate of abnormalities from this incubation treatment (Hare *et al.*, 2002). This result is congruent with previous research, which has demonstrated a negative influence of incubation temperature extremes on survival and phenotype on reptiles (Noble et al., 2018), highlighting the importance of considering incubation regimes when designing translocation programmes; individuals should not be incubated at temperature extremes, and if they are, should not be released due to reduced likelihood of translocation success.

As we predicted, the captive-reared Suter's skinks translocated to Korapuki Island have met two of Miller *et al.*'s (2014) four criteria that indicate translocation success: survival and growth, and evidence of reproduction. Individuals increased in body size throughout the course of our seven year study, reaching maturity by 2005 when the first recaptures commenced. By this stage, most females were gravid with one or more eggs. Thus, this translocation can be tentatively deemed successful. Wild individuals translocated from Green Island to Korapuki Island have met all of Miller *et al.*'s (2014) criteria for success (Towns & Ferreira, 2001; Miller *et al.*, 2011, 2014), with population growth detected within 3 years of release (Towns & Ferreira, 2001), and juveniles representing approximately 25% of the consistently high number of individuals captured since 2000 (e.g. 168 captured in 2006 from 30 founders released in 1992) during biennial monitoring (Miller *et al.*, 2011, 2014). However, Towns & Ferreira (2001) cautioned that at least 20 years may be required before translocation success can be declared. Nonetheless, the success rate of translocations for captive-reared lizards has rarely been monitored and evaluated (e.g. Towns *et al.*, 2016a). As such, our case study provides valuable information that can inform future translocation efforts.

Captive-reared and wild individuals sprinted at equivalent speeds

Our study presents important data on the performance of captive-reared skinks in the wild compared to that of wild-born individuals (Miller *et al.*, 2010). Sprint speed of captive-reared males 5 years post-release was similar to that of wild males. Our result was unexpected in light of previous studies on *Oligosoma* skink species in which sprint speeds of captive-reared lizards were considerably slower than those of wild individuals (Connolly & Cree, 2008; Hare *et al.*, 2012). The slower speed has previously been attributed to heavier body mass of captive-reared skinks (Connolly & Cree, 2008;

Hare *et al.*, 2012), reduced fear of humans or physiological changes owing to the restricted size of enclosures (Hare *et al.*, 2012). These factors are unlikely to have influenced lizards in our study since they were not captive at the time of trials and had 5 years in the wild to develop their sprinting ability. The similarity between captive-reared and wild-born males in our study could represent a bias towards faster captive-reared adults if 1. sprint speed at 4 months, which did not affect survival probability, is not predictive of adult speed, and 2. adult survival is influenced by locomotor ability, resulting in only the fastest captive-reared males surviving to recapture. Alternatively, maximum sprint speed in this species may simply not be a fitness-related trait. Instead, the proportion of maximum speed used in nature, or ecological performance, could be more biologically relevant, and the trait upon which selection acts (Irschick & Garland, 2001; Irschick, 2003; Husak, 2006). For example, Husak (2006) found that survival of yearling and adult collared lizards (*Crotaphytus collaris*) was dependent on the speed used by individuals to escape predators, irrespective of their maximal sprinting capacity. Likewise, Hoskins *et al.* (2017) proposed that the low repeatabilities of sprint speed in the closely related shore skinks (*O. smithi*) could indicate that skinks were not performing at their maximum capacity in field trials.

Diving was inhibited in captive-reared males

Only 40% (all female) of captive-reared skinks dived in one or more dive trials (*cf* 89% in Korapuki Island wild-born skinks: Miller *et al.*, 2010), and while the proportion of females that dived was similar to the wild lizard average (89% of skinks dived in at least one trial), their dive durations (22–186 s) were shorter than, or in the lower range of, dive durations by wild-caught lizards (71–1229 s: Miller *et al.*, 2010). The willingness to dive may reflect predator escape behaviour in gravid females (Miller *et al.*, 2010) since gravidity impedes sprint speed in lizards (Shine, 1980; Cooper *et al.*, 1990). While the effects of small sample size cannot be discounted, it is possible that avoidance of diving by males and shorter dive durations by females were due to a lack of opportunity to acquire diving skills during crucial stages of development. Whatever the reasons for the diving behaviour observed here, our results imply a generally negative impact of captivity on diving behaviour in Suter's skinks, though additional research is needed to elucidate this further.

Conclusions

Our study has shown that the traits associated with post-translocation success may not always be intuitive, and could potentially be influenced by adaptation to captivity. We found that larger, leaner skinks had greater survival, suggesting that these should be preferentially selected for translocations of this species, and that sprint speed of captive-reared individuals was equivalent to that of wild-born lizards. Our

study demonstrates the importance of long-term monitoring of translocated populations in order to ascertain success rates and identify key traits that positively influence translocation success. In turn, the most suitable candidates for future release can be determined. Similar quantitative assessments should be a fundamental component of future translocations globally.

Rearing animals in captivity until they attain a size where they are less likely to succumb to predation or starvation through the critical neonatal period (Ferguson *et al.*, 1982) can improve survival post-release (Ferguson et al., 1982; Escobar et al., 2010). However, captive conditions can influence phenotype in ecologically relevant ways (Burghardt (2013); Snyder *et al.*, 1996; Connolly & Cree, 2008), and this must be addressed when establishing captive management programmes. Certainly, captive rearing should be considered a last resort option only, and not all species are suitable for captive conditions. For example, western populations of grand (*O. grande*) and Otago skinks (*O. otagense*) experienced poor survival and breeding in captivity (Hare *et al.*, 2019). Therefore, where captive management is deemed appropriate, breeding facilities should provide ample opportunity for lizards to acquire the skills necessary to maximize survival post-release. To that end, large enclosures comprising a variety of structurally complex microhabitats that closely mimic wild conditions, and allow individuals to display natural foraging, antipredator and social behaviours, should be established. For example, semiaquatic species would benefit from access to deep water to acquire diving skills, whereas arboreal species would benefit from climbing apparatus of different structures.

Acknowledgements

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