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# Habitat suitability for conservation translocation: The importance of considering camouflage in cryptic species



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#### ABSTRACT

Habitat suitability is a critical aspect for the successful establishment of a translocated population. Past studies have identified multiple factors that contribute to habitat suitability, including resource availability, presence of invasive species, landscape connectivity and climate. However, visual camouflage – coloration that conceals individuals from predators or prey – is another important ecological requirement that has been largely overlooked. We provide a case study to illustrate how color patterns of a prey species can change from that of the source site following translocation. Shore skinks (*Oligosoma smithi*) were moved from a coastal sand dune ecosystem to an offshore island beach that differed in substrate and color. Within one year following release, the translocated population's color pattern variation had reduced to mostly one pattern type. The high match in color patterns between the skinks and release site (including a new substrate type) may have contributed to the observed color pattern shift. This reduced variation in color pattern implies that not all founders survived, potentially decreasing the genetic diversity in the population. Our study highlights the importance of considering a species' camouflage requirements when selecting habitat for release, not only to maximize founder survival and establishment success, but also to maintain phenotypic and genotypic diversity in the long-term.

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### 1. Introduction

In conservation translocations, habitat suitability is of critical importance for the successful establishment of a population (Germano and Bishop, 2008; Wolf et al., 1998). A suitable, good quality habitat promotes survival and breeding of a newly founded population. In contrast, poor habitat quality at release sites has been shown to incur significant post-translocation losses; for example, 16%–50% of failed cases are associated with poor habitat quality (Brichieri-Colombi and Moehrenschlager, 2016; Germano and Bishop, 2008; Moehrenschlager et al., 2013; Wolf et al., 1996). However, what constitutes habitat quality, and the specific reasons of translocation failure, are often unclear (Ewen and Armstrong, 2007; Fischer and Lindenmayer, 2000; Wolf et al., 1996). Therefore, identifying the ultimate causes for translocation failure due to a 'poor quality' site can be challenging.

Factors that determine habitat suitability or 'quality' are speciesspecific (Ewen et al., 2014). Selecting suitable habitat will depend on understanding the critical ecological requirements for the species in question, as well as the species function within the ecosystem or food web. Previous studies have looked at habitat or landscape

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characteristics that fit species' requirements for foraging, refuge use, egg-laying sites (Castilla and Swallow, 1995; Ebrahimi and Bull, 2012; Ortiz-Catedral and Brunton, 2009), dispersal or other behaviors (Armstrong and Ford, 2015; Gobiel and Villard, 2008; Parlato and Armstrong, 2013; Richardson et al., 2015; Stamps and Swaisgood, 2007), effect of invasive or anthropogenic threats (e.g., removal of introduced predators, or isolation from the public; Atkinson, 2002; Moseby et al., 2015; Norbury et al., 2014; Towns, 2011; Towns et al., 1997). and climatic differences between sites (e.g., climate change, Fordham et al., 2012; Schwartz and Martin, 2013). In addition to the above, for some species the need for camouflage may be critical for survival, either to avoid predators or to successfully capture prey. The efficacy of visual camouflage is often dependent on the matching of the animal's body color to its immediate background (Merilaita and Stevens, 2011; Stevens and Merilaita, 2011a). Therefore, a potential mismatch between the animals and their new environment may increase their conspicuousness to predators or prey.

Three main factors influence effective background-matching in cryptic animals (Houston et al., 2007; Merilaita et al., 2001): 1) phenotypic plasticity and genetic variation of the focal species (e.g., Bergstrom et al., 2012; Cortesi et al., 2015; Morgans and Ord, 2013; Rosenblum, 2005; Tyrie et al., 2015; Westley et al., 2013); 2) the abundance and species composition of predators or prey (e.g., Defrize et al., 2010; Llandres et al., 2011; Rohwer and Paulson, 1987; Stankowich and Coss, 2007;

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Théry et al., 2004; Troscianko et al., 2013); and 3) the color, structure and complexity of the habitat (e.g., Kekäläinen et al., 2010; Nafus et al., 2016; Nafus et al., 2015). Because each factor influences an animal's conspicuousness across time and space, any change in these factors due to translocation could impact the population at different levels. For example, a population that mismatches with their release site can have lower establishment of founders through reduced individual fitness (inability to hide from predators or to capture prey). Lower founder size will affect recruitment rate, and the phenotypic and genotypic diversity of the translocated population (Armstrong and Wittmer, 2011; Forsman, 2014; Miller et al., 2009; Thrimawithana et al., 2013).

How significant a problem can ineffective camouflage be on the outcome of conservation translocations? We cannot currently assess this quantitatively for human-mediated translocations due to a lack of relevant data from the translocation outcomes, although the potential effects of human-induced disturbances on threatened-species' camouflage was raised within a recent literature review (Delhey and Peters, 2016). Nevertheless, a few studies have highlighted the potential effect of camouflage on the fitness of translocated species. One study on Atlantic salmon (Salmo salar) translocated for economic purposes showed a significant decrease in individual survival and higher predation scars on salmon at mismatched background sites (Donnelly and Whoriskey, 1993). The authors noted the importance of color-matching to minimize likelihood of individual loss to predators. Additionally, experimental and field studies on desert tortoises (Gopherus agassizii) found that the availability of rocks at a site contributed to reduced predator detection and lowered the dispersal of juveniles from the release site, thereby increasing individual fitness of the tortoises (Nafus et al., 2016; Nafus et al., 2015). Authors emphasized the importance of linking habitat to camouflage behavior (i.e., individual fitness) when selecting suitable habitat for species conservation management.

Here, we present a case study that illustrates how color pattern, and therefore the degree of background-matching of a population, can change post-translocation without population management. We quantified color pattern variation and background-matching of a cryptic prey species before and after translocation. We also observed the degree of matching of the population when released to a site that included novel substrates. Our case study shows that color pattern of a translocated population can significantly differ from the source, even within one generation, and highlights the potential significance of camouflage on the phenotypic diversity of a translocated population.

#### 2. Materials and methods

#### 2.1. Study species and study sites

The shore skink (Oligosoma smithi) is a New Zealand endemic (national conservation status: Not Threatened, Hitchmough et al., 2013) with a relatively wide geographic distribution, inhabiting the northern half of the North Island. This species is present in diverse coastal habitats, from sand dunes, sandy, rocky pebbles or boulder beaches to vegetated cliffs on the mainland and offshore islands (Towns et al., 2002). There is extensive color pattern variation in this species among populations, with island populations having less variation overall compared to the mainland (McCallum and Harker, 1982; Towns, 1972). It is not known if color patterns of shore skink are genetically determined. Within their coastal habitat, shore skinks are found close to high tide mark of the coastline to > 1 km inland; (Towns, 1975). Their home range and dispersal behavior is unknown, but because of the small size of the skinks (i.e., adult snout-vent length, SVL = 50-70 mm), we expect movement to be small. Similar to other New Zealand native reptile species, natural predators for shore skinks are birds (van Winkel and Ji, 2012), and populations are also affected by introduced mammals such as cats, rats, hedgehogs and mice (Jones et al., 2005; Lettink and Cree, 2006; Norbury et al., 2014; Wedding, 2007). Some populations are able to persist in non-predator controlled sites (M. Baling personal observation; Towns, 1996). As part of a conservation effort to restore reptile diversity at an island reserve in the Auckland region (Baling et al., 2013), shore skinks were translocated from the nearest mainland population.

We sourced skinks from Tāwharanui Regional Park (hereafter 'Tāwharanui'), a 550 ha peninsula protected by predator-proof fencing erected in 2004. All introduced mammal species were eradicated following an aerial drop of poison in the park except for three species (house mice Mus musculus, European rabbits Oryctolagus cuniculus and European hedgehogs Erinaceus europaeus, Maitland, 2011). As a consequence, the population size of the resident shore skinks increased dramatically. The park also has a mixture of introduced (e.g., Australian magpie Cracticus tibicen, common myna Acridotheres tristis) and native (e.g., pukeko Porphyrio melanotus, sacred kingfisher Todiramphus sanctus) predatory birds. In 2006, we collected 40 skinks (14 males and 26 females) from a coastal sand dune system that had a gradient of lightcolored sand at the foreshore to 100% vegetation cover at the back of the dunes. Nine out of the 26 females were recorded gravid at the time of capture. We captured skinks using an existing pitfall trap grid at the site, and also hand-searches by public volunteers, and staff and students of Massey University.

We then released these 40 shore skinks to Tiritiri Matangi Island Scientific Reserve (hereafter 'Tiri') in the Hauraki Gulf, Auckland (Baling et al., 2010). Tiri is a 220 ha public community-led island restoration that has had a highly successful history of translocation of threatened endemic birds, and more recently, reptiles (Baling et al., 2013; Galbraith and Cooper, 2013; Parker, 2013). The island is free of introduced mammals (Graham and Veitch, 2002), and has high densities of bird species, including known native predators of lizards (e.g., sacred kingfisher and morepork *Ninox novaeseelandiae*, van Winkel and Ji, 2012). The island had three extant resident reptile species, two skinks and one gecko (Baling et al., 2013). Shore skinks were recorded in the 1970's but subsequent surveys failed to detect their presence, and so the species was declared locally extinct (Baling et al., 2013).

Shore skinks were released on a small north-facing beach comprised of areas of dark-colored sand at the west and a mix of small and boulder rocks on the east part of the beach. Where the sand and rocks met (in the mid-section of the beach), there was accumulated driftwood and seaweed. Both substrates were mainly bare at the front of beach (with some seaweed and driftwood), and had varying levels of vegetation cover at the back. Vegetation consisted of exotic grasses, followed by thicker bush and trees towards the back of the beach. There were two other resident species present at the site: copper (*Oligosoma aeneum*) and moko skinks (*O. moco*), both are known to co-exist with shore skinks at other sites (Towns, 1972; Towns et al., 2002).

# 2.2. Population surveys

Between February 2007 and March 2008, we monitored populations at Tāwharanui and Tiri every three months. At Tāwharanui, we used three existing pitfall trap grids set at the sand dunes by a previous study (Wedding, 2007; Wedding et al., 2010). The grids were spaced 75 m and 120 m apart along the coastline, with each grid containing 40 4 L-sized plastic pitfall traps spaced every 20 m  $\times$  25 m, for a total of 120 traps for all three grids). At Tiri, we set up two  $6 \times 3$  grids within the sand and rock sections of the beach. The grids had alternating pitfall traps and artificial refuges, spaced c. 5 m apart. These two grids were connected to a line of six pitfall traps in the middle of the beach, where the sand and rock met. For both sites we baited pitfall traps with fish-based cat food, and checked all traps and refuges every 24 h for three trap-nights at Tāwharanui and six trap-nights at Tiri for each survey. We temporarily marked all captured skinks with a xylene-free pen to avoid individual resampling during each survey. After processing, individuals were released at their point of capture.

During surveys, we took standardized digital photographs of the dorsal side of skinks and habitat backgrounds  $(1 \times 1 \text{ m})$  where the

skinks were caught using an Olympus mju 770SW (Olympus, Japan). Each photograph (dorsal or background) included a photographic grey standard (QPcard 101, Sweden) with 18% reflectance. We also photographed founder individuals when animals were caught for translocation in December 2006. Due to the nature of the translocation (i.e., public volunteers were used on the day of captures) not all backgrounds for the founder individuals were recorded or photographed. Overall, we had three groups of skinks: the source, a subset of the founders, and the translocated population (i.e., a mix of survived founders and their offspring).

# 2.3. Quantifying pattern complexity

We used the photographs to score individuals according to the degree of dorsal pattern complexity. We quantified complexity according to pattern elements that are known to influence camouflage: i.e., pattern shapes, number of shapes (diversity) and density of each shape (Dimitrova and Merilaita, 2011; Merilaita and Dimitrova, 2014). Based on these criteria, we assigned individuals to one of four pattern types: (1) plain: no patterns or very weakly patterned; (2) midplain: no or very weak speckling combined with the presence of a mid-dorsal line on >50% of the body length; (3) spot: distinctive dense speckling and no (or <50%) mid-dorsal line on length of body; and (4) midspot: distinctive dense speckling and presence of mid-dorsal line in >50% of the body length (Fig. 1).

# 2.4. Quantifying vegetation cover

We quantified the proportion of vegetation cover within a  $1 \times 1$  m plot of each habitat background where skinks were caught. We divided each photograph into four sections and estimated the proportion of vegetation cover by eye.

# 2.5. Quantifying color from photographs

To quantify color, we scored digital photographs, which capture the majority of the visible spectrum (400–700 nm) but not the ultraviolet (300–400 nm). These are appropriate for shore skinks because they showed minimal ultraviolet reflectance (see online Supplementary Fig. A1). Additionally, the distribution of lizard colors within a RGB color space has been shown to be significantly similar in the avian or lizard visual color space (Smith et al., 2016).

In each photograph, we extracted the averaged mean red (R), green (G), blue (B), and brightness (V) values (ranging from 0 to 255) from

400 random points selected within areas of the body or habitat, and the grey standards. Within each background photograph, we selected two polygon areas similar to the size of skinks and extracted values as above, and averaged the values of the two areas. We then calibrated all values for skink and background using linearization and equalization protocols described in Stevens et al. (2007). Firstly, we determined the relationship between the camera responses to all values (R, G, and B) by photographing a set of grey standards (ColorChecker Classic, X-Rite, USA) with measured reflectance values. We applied a biexponential function (Garcia et al., 2013), to linearize R, G, B and V values to reflectance:

$$y = a * exp.(b * x) + c * exp.(d * x)$$

where, y is the linearized value, and a, b, c, d are empirically derived constants specific to a given camera. Finally, we equalized R, G, B, V values relative to the grey standard in each photographs to remove any effect of variation in lighting.

We calculated the standardized differences between the calibrated R and G channels as x=(R-G)/(R+G+B), and between G and B channels as y=(G-B)/(R+G+B) to obtain a two-dimensional representation of color space, where the distance from origin represents saturation, and the angle relative to the axis is hue (Endler, 1990). We calculated saturation (S) as  $S=(x^2+y^2)^{\frac{1}{2}}$  where x and y represents the standardized difference of R-G and G-B channels, respectively.

# 2.6. Statistical analyses

We investigated body pattern variation by comparing the proportions of each pattern type between three populations: source (Tāwharanui), the subset of founders from Tāwharanui, and translocated (Tiri). We used Fisher's exact test to determine whether the proportion of the pattern types in the founder and translocated populations differed significantly more than expected by chance. We conducted post-hoc binomial tests to identify the specific pattern types that differed between the populations.

To ascertain the baseline association between pattern complexity of skinks and vegetation cover, we plotted 95% confidence intervals (CI) of means for the percentages of vegetation cover (arc-sin transformed) against body pattern types of the source population. We used the degree of overlap between CI of the pattern types as a measure of significant differences from one another (p < 0.05). Additionally, we calculated the magnitude of effect sizes between pattern types using a standardized mean difference, unbiased Cohen's d (Morgans and Ord, 2013).



Fig. 1. The four dorsal body pattern types assigned to shore skinks at Tawharanui Regional Park. From left to right: plain, midplain, spot, and midspot.

These values and their CI were then converted to r values (Nakagawa and Cuthill, 2007; Ord et al., 2011; Ord and Stamps, 2009) to provide a familiar effect size metric (r=-1 to 1) that functions similarly to correlation coefficient (Ord and Stamps, 2009). Any CI of r that did not overlap with zero was considered to be a biological effect. We also applied this approach for comparison within the founder and translocated populations. Due to the occurrence of two different substrate types at the Tiri population, rock and sand, we analyzed data for the two substrates separately.

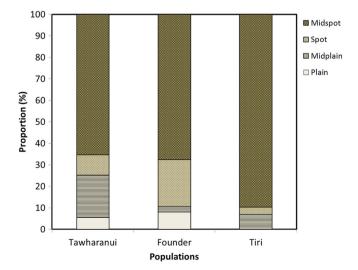
As the skinks varied primarily in saturation and brightness, we only assessed matching between skinks and their backgrounds of these two values. We conducted a power transformation for brightness ( $\lambda=-0.5$ ) and saturation ( $\lambda=0.5$ ) to achieve normalization of data. For the source population, we determined the association between skink brightness or saturation and vegetation cover or background brightness and saturation using linear regressions.

To measure if there was an overall difference in habitat color (brightness and saturation) between Tāwharanui and Tiri, we compared the mean, CI and standardized mean difference (using *r*-values; Morgans and Ord, 2013; Ord and Stamps, 2009) between the backgrounds occupied by skinks. We looked at the difference between background and skink to determine the degree of background-matching for each pattern type at source population to the backgrounds of Tāwharanui. Due to the dominance of one pattern type in the translocated population, we only compared background-matching for pattern type midspot between all populations.

#### 3. Results

#### 3.1. Body pattern variation and habitat use

The founder population had midspot as the most common pattern type (67.6%, n=25), followed by spot (21.6%, n=8). The proportions of founders with the other two pattern types were low (Fig. 2). When compared to the founder, the distribution of pattern types in the translocated population at Tiri was significantly different than expected by chance (Fisher's exact test, p=0.03, n=37, 29). Specifically, the proportion of midspot was higher (89.7% vs. 67.6%, binomial test, p<0.01, n=26, 25) while spot was lower (3.4%, vs. 21.6%, binomial test, p=0.03, n=1, 8) at Tiri than expected given the observed proportions in the founder population (Fig. 2). The plain pattern type was not present at the translocated population.



**Fig. 2.** Proportion of four dorsal pattern types (plain, midplain, spot, midspot) in three shore skink populations: Tāwharanui Regional Park (n=337), subset of the founders (n=37), and translocated population at Tiritiri Matangi Island (n=29).

The distribution of the body patterns varied in relation to vegetation cover at the source population (Fig. 3). Plain individuals occupied habitats with significantly lower vegetation cover (<70%) compared to the other three types (plain-midplain r=0.33, plain-spot r=0.36, plain-midspot r=0.38; vs. midplain-spot r=0.02, midplain-midspot r=0.22). Midspots were primarily found in over 90% vegetation cover. We observed a difference in occupancy for pattern types between the two substrates at Tiri (translocated population). The majority of individuals (i.e., midspot) caught on sand were in over 90% vegetation cover (Fig. 3c), similar to the source population. However, it was the opposite for the novel substrate, rock, where all midspots were caught in <20% vegetation cover. Full comparisons of vegetation cover occupied between pattern types for each population (effect sizes) are provided in online Supplementary Table A2.

At Tāwharanui, background saturation increased ( $r^2=0.091$ , p<0.01) while brightness decreased with increasing vegetation cover ( $r^2=0.605$ , p<0.01). Therefore, high vegetation cover had most intense and darkest background color compared to low vegetation covers. The habitats occupied by skinks at Tāwharanui and Tiri differed significantly in saturation but not in brightness. Saturation was greater at the highly vegetated Tiri sand (S=0.37, CI 0.309-0.439) and less in more open areas of Tiri rock (S=0.09, CI 0.061-0.119) compared to the source population at Tāwharanui. The mean difference for saturation was greatest within Tiri, between sand and rock (r=0.87). Full comparisons of effect sizes for color between sites are provided in online Supporting Table A3.

# 3.2. Background-matching of shore skinks

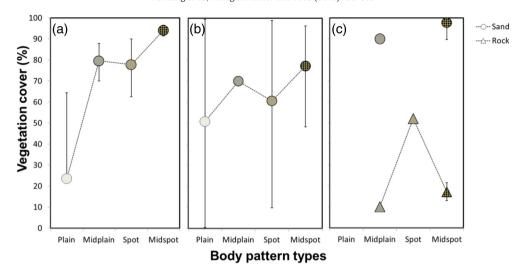
The color of skinks was generally lighter ( $r^2 = 0.09$ , p < 0.01) and less saturated ( $r^2 = 0.074$ , p < 0.01) than that of the available backgrounds (Fig. 4). There was an increase in the discrepancy between the brightness of skinks and their background as pattern complexity increased (Table 1; Fig. 4a), with midspots showing the greatest mismatch to the background at Tāwharanui and on the sand background at Tiri. Midspots were most matched to their background at Tiri rock, and least matched at Tiri sand in terms of both brightness and saturation (Table 1; Fig. 4).

#### 4. Discussion

Our study provides evidence that when habitat differs from the source location, color patterns of cryptic prey can alter within a short period of time following translocation. Overall, we saw a marked effect on the color patterns of shore skinks translocated to Tiri, where there was reduced variation in body patterns favoring almost exclusively one type. This shift in color patterns did not seem to have an apparent negative effect on habitat use of the Tiri population because within one year, individuals were able to adapt and utilize a new substrate (rock) that was not present at the source coastal sand dunes of Tāwharanui. The high match (in terms of brightness and saturation) between the surviving skinks to rock (with low vegetation cover) may have contributed to the successful transition to the new substrate. But we suspect a reduced number of founder individuals survived, and discuss the consequences (i.e., reduced genetic diversity) of this strong selection for inconspicuous color patterns.

# 4.1. Change in color pattern types

Out of the four body pattern types from the mainland source population, only one was dominant at the island release site. Midspots had the most complex pattern, and were the darkest variant of the four types, so it may have had an advantage in the darker and highly vegetated environment at Tiri (see below). But midspot was also the most abundant type within the source and founder populations, so we cannot rule out a founder effect, with the midspot variant being fixed (and the

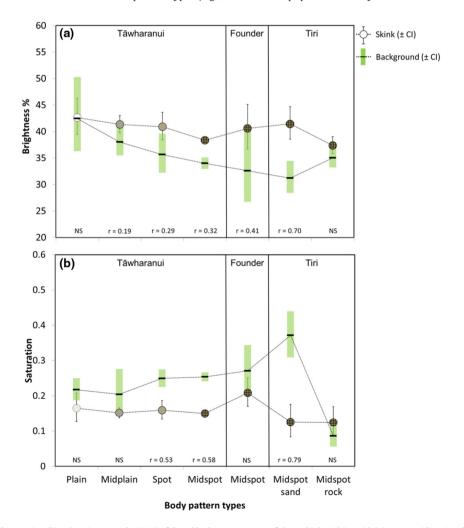


**Fig. 3.** Dorsal body pattern types of shore skinks (plain, midplain, spot, midspot) occupying different percentages of vegetation cover (mean and 95% Cl) at three populations: (a) source at Tāwharanui Regional Park (n = 337), (b) subset of founders from Tāwharanui (n = 19), and (c) translocated population at Tiritiri Matangi Island (sand n = 15, rock n = 14).

rare plain pattern type lost) in the founder population due to chance. As yet, we do not know the degree of heritability, survivorship, alternative functions (e.g., thermoregulation, social signaling), or whether there are breeding or behavioral differences between the color pattern types (e.g.,

Clusella-Trullas et al., 2007; Keren-Rotem et al., 2016; Olsson et al., 2013; Scali et al., 2012; Stuart-Fox and Moussalli, 2009).

Nevertheless, we still expected to observe higher variation at Tiri because the population surveyed was a mix of founder and first generation



**Fig. 4.** Mean brightness (a) and saturation (b) values (mean and 95% CI) of dorsal body pattern types of shore skinks (plain, midplain, spot, midspot) and habitat background of source population at Tāwharanui Regional Park, compared to midspot individuals of the founder population, and translocated population at Tiritiri Matangi Island. *r* is the effect size for standard mean difference between dorsal and background colors. Difference is not significant (*p* > 0.05) when CI of means for skink and background overlap (NS).

**Table 1**The standard mean differences in color (brightness and saturation) between three shore skink populations: source and subset of founder populations from Tāwharanui Regional Park, and translocated populations at Tiritiri Matangi Island (two substrate types).

Population	Comparison with background	Effect size, <i>r</i> (lower CI, upper CI)	n <sub>body,</sub>
Brightness			
Tāwharanui	Plain	0.01 (-0.307, 0.322)	19, 16
	Midplain	0.19 (0.014, 0.347)*	65, 58
	Spot	0.29 (0.043, 0.495)*	31, 27
	Midspot	0.32 (0.228, 0.401)*	218, 177
Founder	Midspot	0.41 (0.031, 0.662)*	13, 9
Tiri – sand	Midspot	0.70 (0.444, 0.826)*	13, 12
Tiri – rock	Midspot	0.38(-0.014, 0.635)	12, 12
Saturation			
Tāwharanui	Plain	0.32 (-0.007, 0.560)	19, 16
	Midplain	0.15 (-0.023, 0.316)	65, 58
	Spot	0.53 (0.326, 0.673)*	31, 27
	Midspot	0.58 (0.517, 0.636)*	218, 177
Founder	Midspot	0.40 (-0.010, 0.655)	13, 9
Tiri – sand	Midspot	0.79 (0.588, 0.874)*	13, 12
Tiri – rock	Midspot	0.30 (-0.096, 0.578)	12, 12

CI's that do not overlap with zero are significantly different at p < 0.05.</p>

island-born individuals. At least 35% of the founder females, consisting of all four pattern types, were gravid at the time of capture at the source. As captive wild-born females give birth to an average of four live young (2–6 young) annually (M. Baling unpublished data), we estimated about 36 neonates to be born within the first three months following release. Therefore, we expected that the first generation offspring born on Tiri (but sired by males from Tāwharanui) would contribute a higher color pattern variation in the translocated population. Despite this, our field observations showed higher than expected occurrence of midspot within one generation.

Interestingly, the presence of a single color pattern type at Tiri corresponds to other naturally-occurring shore skink populations on offshore islands with rocky or boulder shorelines bordered by vegetation (M. Baling personal observation; McCallum, 1980; McCallum and Harker, 1982; Towns, 1972; Towns and Hayward, 1973). These populations have no or very low phenotypic variation (e.g., plain dark to almost black, with sparse speckling). The reason for this low variation on offshore islands is unknown, but for our one-year study, we suggest as likely causes bird predation pressure (van Winkel and Ji, 2012) coupled with specific habitat characteristics.

# 4.2. Habitat occupancy by shore skinks

Shore skinks at Tiri occupied both highly vegetated sand areas (similar to the Tāwharanui population), and novel rock substrates, mainly in areas of low vegetation cover (<50%). Despite the availability of rock with high vegetation cover (up to 100%) we did not sight or catch shore skinks within that part of the survey grid. This distribution in pattern types among substrates could also be influenced by behavioral preference of the skinks. Habitat choice to improve camouflage has been observed in other species (e.g., Ahnesjö and Forsman, 2006; Cooper and Sherbrooke, 2012; Marshall et al., 2016; Morey, 1990; Nafus et al., 2015), but needs to be confirmed for shore skinks.

Another potential influence on the occupancy of shore skinks at the release site is competition with resident species. Moko and copper skinks have been seen or caught in the survey grid, including in highly vegetated rock areas. Interspecific competition (either through territorial aggression or spatial displacement) between shore skinks and resident species at the release site is unknown but possible (Baling et al., 2013). However, anecdotal observation of the general distribution of the three species at the site during our surveys did not appear to differ from populations on other islands with rocky beaches (McCallum and Harker, 1982; Towns, 1972). Shore skinks at these islands have been recorded using rock or boulder beaches edged by vegetation.

#### 4.3. Background-matching of shore skinks

The degree of background-matching for midspot was dependent on substrate type. Individuals mismatched with the dark, saturated 'brown-green' of highly vegetated habitat with sand substrate at both source and release sites. This mismatch could be compensated by the high vegetation cover, which provides greater visual complexity (in shape diversity, size and spatial density; Dimitrova and Merilaita, 2010; Dimitrova and Merilaita, 2011, 2014; Sherratt et al., 2007; Xiao and Cuthill, 2016) and visual obstruction or physical protection, thus making detection more difficult. In contrast, midspots were highly matched to the dark grey and simpler backgrounds of rock. Similarly, plain patterned individuals matched the low or no vegetation sand dunes of Tāwharanui. The low visual complexity of low vegetation cover habitats is likely to increase reliance on background-matching. Other studies have also suggested that such simple or uniform backgrounds promote the evolution of accurate color background-matching in prey (Houston et al., 2007; Merilaita et al., 2001; Sherratt et al., 2007).

Due to the small sample size of the other three pattern types, we are unable to determine if their degree of background-matching was related to survivorship at Tiri. However, we suggest that midspot had a higher probability of survival compared to the other pattern types for two reasons: 1) likelihood of background-matching at the release site, and 2) habitat availability. Firstly, of all pattern types at Tāwharanui, midspot provided the closest color and pattern match to the Tiri backgrounds. Secondly, the lack of bare sand may have considerably reduced the chances of survival of the plain pattern type at Tiri. We did not quantify habitat availability in this study but areas with <20% vegetation cover occurred in 20% of our survey grid (4.15 ha) at Tāwharanui (C. Wedding, unpublished data; Wedding, 2007). Compared to the smaller-sized beach at Tiri (0.15 ha), vegetation covered most of the sand area down to high-tide level, so there was a lot less bare ground area available at Tiri compared to Tāwharanui.

# 4.4. Diversity in translocated populations

The shore skink founders have successfully survived to produce off-spring on the island, but the diversity of the population appears reduced based on the observed color patterns of the survived individuals. If we assume that the color patterns of shore skinks are inherited, the observed biased frequency of midspot in the population may indicate reduced genetic diversity, due to poor survival of mismatched founders or their offspring. This loss in diversity for one population may not be significant for a widely distributed species like the shore skink, but may be detrimental to a rare species. The importance of maintaining diversity will depend on the management objectives for the species; whether conservation priority is to increase the number of individuals, or to maintain their genetic diversity (e.g., Towns et al., 2016). This can then influence the management decisions for both population and release site selections (Ewen and Armstrong, 2007; Ewen et al., 2014).

Ideally for cryptic species, the range of substrate color and complexity of habitat at the release site should match that in the source population to maintain effective camouflage. This is particularly important for cases of populations living in low complexity habitats, where accurate background-matching is critical for founder survival. If the options for habitat choice are limited and if color pattern variation is high at the source, a larger founder population size (i.e., high phenotypic and genotypic diversity) should be released at the site. This is because high phenotypic diversity such as color patterns in prey can provide protection against predators at both individual and population levels (Forsman, 2014; Karpestam et al., 2016). However, if the population size at the source is low (e.g., rare or highly threatened species), losing valuable individuals can have significant negative impact. For such species, the conservation objectives generally include increasing the number of breeding animals, and high survival of individuals during and posttranslocation. To this end healthy animals, representing genetic

diversity are often selected. We suggest that conservation translocations of cryptic species also consider the phenotypes of the founder individuals that would best match habitat available at the release area. This will ensure minimal disruption of the relationship between released founder individuals and their environment at the establishment phase of the translocation.

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#### Supplementary data

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# Glossary

Conservation translocation: intentional movement of a living organism from one location to another for the main purpose of conservation, either to improve the conservation status of a species, or to restore ecosystem function or processes (IUCN/SSC, 2013).:

Background-matching: a concealment strategy in which an organism avoids detection or recognition by resembling its immediate background in color patterns (Endler, 1978; Stevens and Merilaita, 2011b).: