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Evaluation of trial reintroductions of two extinct in the wild reptile species on Christmas Island

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Abstract

Conservation reintroductions play a vital role in the recovery of threatened species, and clear goals and objectives are essential for evaluating their effectiveness. In this study, we assessed short-term success (<18 months) of trial reintroductions of the Extinct in the Wild blue-tailed skink (*Cryptoblepharus egeriae*) and Lister's gecko (*Lepidodactylus listeri*) on Christmas Island. Our evaluation criteria focused on body condition, reproduction, habitat suitability, survival and population growth. In 2018 and 2019, 170 *C. egeriae* and 160 *L. listeri* were translocated from a local captive breeding facility to a 2600 m^2 outdoor fenced enclosure designed to exclude a predatory snake. Despite body condition declining immediately following release for both species, it had improved by 6 months post-release. We also detected successful reproduction in both species. Apparent survival was high for *C. egeriae* but low for *L. listeri*, and population growth was only evident in *C. egeriae*. We were unable to determine whether low survival of *L. listeri* in the release site was due to high post-release dispersal (beyond the exclosure) or mortality. Both species selected habitats that contained high rock and log cover and avoided areas with low ground cover. Appropriate assessment criteria, as utilized in this study, enable objective and timely evaluations of reintroduction success, thereby facilitating the improvement and refinement of reintroduction protocols. Our study showed that *C. egeriae* can establish (in the short- to medium-term) in a site from which a principal threat has been excluded and undergo rapid population growth, whereas under current conditions *L. listeri* cannot. However, we also demonstrate that such medium-term success may not lead to long-term success, as the rapid increase in *C. egeriae* population was reversed between 29 and 31 months after release because the barrier used to exclude an invasive predator, the wolf snake (*Lycodon capucinus*), was breached.

Introduction

Conservation reintroductions are increasingly used to recover threatened species (Seddon, Armstrong, & Maloney, 2007; Armstrong & Seddon, 2008), especially when ecosystem protection and habitat restoration are insufficient to reverse population declines (Bennett *et al.*, 2012). Reintroductions involving reptiles are far less common than those involving other vertebrates (Dodd & Seigal, 1992; Fischer & Lindenmayer, 2000). Despite some notable successes (Fitzgerald *et al.*, 2015), reptile reintroductions have often failed, which has been linked to poor habitat suitability, failure to address the original cause of decline, too few animals released and rapid dispersal from release sites (Griffith *et al.*, 1989; Wolf *et al.*, 1996; Germano & Bishop, 2009). In response to these challenges, reintroduction managers are encouraged to incorporate well-designed experiments and scientific rigor into reintroduction programs (Armstrong & Seddon, 2008; Kemp *et al.*, 2015). However, reintroduction experiments involving threatened species are often not possible due to limited availability of founder animals and high-quality habitat, challenges with the effective control of major threats and inadequate resources for monitoring (Kemp *et al.*, 2015). In such cases, trial (unreplicated and uncontrolled) reintroductions can be valuable for establishing feasibility, for providing preliminary data to determine the likelihood of reintroduction success more broadly and for honing methodologies to improve such likelihood (Seddon, Armstrong, & Maloney, 2007; Watts *et al.*, 2017).

Most reintroductions aim to establish self-sustaining or free-ranging populations (Seddon, 1999) or maintain persistent populations (Armstrong & Seddon, 2008). However, much assessment of reintroduction success and failure has been conducted without clear goals and objectives, within short timeframes, or in the absence of relevant biological and ecological information (Soorae, 2010; McCoy *et al.*, 2014). To address this, it is desirable to set *a priori* success criteria at specific time points: such criteria include assessing percentage survival after 1 month, evidence of reproduction within 6 months and population persistence after 5 years, (Bertolero & Oro, 2009; Moseby *et al.*, 2011; McCoy *et al.*, 2014). These criteria can be tailored to species' life cycles and allow for targeted monitoring, even though they may not reliably predict or directly influence the long-term persistence of the population (Soorae, 2010; Sutherland *et al.*, 2010).

In this study, we describe two reintroduction trials of the blue-tailed skink (*Cryptoblepharus egeriae*) and Lister's gecko (*Lepidodactylus listeri*) on the Australian external territory of Christmas Island (135 km^2) in the Indian Ocean. Both species are recognized as Extinct in the Wild (Woinarski *et al.*, 2017), but remain listed as Critically Endangered under the Australian Environmental Protection and Biodiversity Conservation Act (EPBC 1999). These reptiles are endemic to Christmas Island and were widespread until the late 1980s (Cogger, Sadlier, & Cameron, 1983) but rapidly declined throughout the 1990s and 2000s, with the last wild sighting of *C. egeriae* occurring in 2010 and of *L. listeri* in 2012 (Smith *et al.*, 2012). Limited studies were conducted during the decline to determine the causes, but predation from invasive species, particularly the common wolf snake (*Lycodon capucinus*), that arrived on Christmas Island in the mid-1980s, was the most likely causal factor (Smith *et al.*, 2012; Emery *et al.*, 2021a,b).

Before their extinction in the wild, Parks Australia initiated a captive breeding program to establish populations on Christmas Island and at Taronga Zoo in Sydney (Andrew *et al.*, 2018). The captive breeding efforts were successful, resulting in population increases from 67 *C. egeriae* and 43 *L. listeri* to over 1000 individuals of both species across the two locations within 8 years (Andrew *et al.*, 2018). Based on this success, Parks Australia implemented a reintroduction trial of *C. egeriae* on Christmas Island in 2017, with animals sourced from the captive breeding colony on the island. As the main factor contributing to reptile declines, namely *L. capucinus*, could not be controlled at the landscape level, *C. egeriae* were released into a 2600 m^2 exclosure constructed to exclude *L. capucinus* and other introduced predators. This initial trial was unsuccessful, with no individuals remaining 6 months post-release (Emery, 2021). The trial likely failed due to inappropriate habitat and unexpected predation by the introduced giant centipede (*Scolopendra subspinipes*) which had not been successfully excluded from the release site (Emery, 2021; Emery *et al.*, 2021a,b).

This paper describes the result of a subsequent (second) reintroduction trial for *C. egeriae* and a first trial for *L. listeri*. We aimed to determine whether captive-bred individuals of *C. egeriae* and *L. listeri* can survive and successfully breed upon release into a semi-wild exclosure on Christmas Island. We present results from the first 15 months post-release, focusing on short-term survival, population dynamics, habitat use and body condition. We then assessed the success or failure of the reintroductions of each species by comparing our findings against predetermined short- and medium-term success criteria. Our findings provide initial insights into the extent of persistence of these two highly imperilled lizard species within a wild context, allowing for potential methodological refinement of future conservation actions.

Materials and methods

Goal and success criteria

The primary objective of both reintroductions was to establish viable, self-perpetuating populations. To monitor progress, we developed short, medium and long-term success criteria modified from (Bertolero & Oro, 2009; Miller, Bell, & Germano, 2014) (Table 1). Timelines for long-term success criteria have not yet been met, so we only address short- and medium-term criteria here. Due to limited research on these species in the wild, our criteria are based on observations from captive breeding, authors' prior knowledge and the unsuccessful reintroduction attempt of *C. egeriae* in 2017 (Emery, 2021). The framework is based on that developed by Armstrong & Seddon (2008) and provides a systematic approach to incorporating success criteria into key questions for both population establishment and persistence. Thus, our criteria for body condition, evidence of reproduction, habitat suitability and post-release survival are associated with population establishment, whilst reproduction, habitat suitability, long-term survival and population growth relate to population persistence (Table 1).

Reintroduction site

The reintroduction site was in plateau forest within a phosphate mining rehabilitation field (Fig. 1). Previous studies by Cogger, Sadlier, & Cameron (1983) indicated that *C. egeriae* and *L. listeri* were sympatric and found in various habitats, including primary and secondary rainforest, coastal vine thicket and rehabilitated phosphate mining areas (such as the site selected for this reintroduction attempt).

The area had been actively restored by Christmas Island National Park staff for approximately 5 years prior to the first reintroduction in April 2017. Restoration efforts included

Table 1 Success criteria and justification for trial reintroductions of *Cryptoblepharus egeriae* and *Lepidodactylus listeri*

Success criterion	Justification
Short (1 month): Body condition After 1-month post-release, body condition has not decreased by more than 10%	When lizards from captive breeding programs are released, they must acclimatize to new environmental conditions and may experience loss of body condition. This is particularly true of captive animals that undergo profound change in conditions such as foraging opportunities, stress of release and new predators. If the release site is suitable, lizards should not lose weight. Thus, a criterion of success for these reintroductions is that individuals do not lose more 10% body condition between release and 1 month after release.
Short (1 month): Survival $>$ 50% of original founders.	A population can only establish when survival and reproduction exceeds mortality and emigration. After acclimatization, it is expected that survival rates should be similar to those of natural populations. Thus, the criterion for success is high founder survival ($>$50%) in the first-month post-release
Short (0–6 months): Reproduction Within 6 months post-release, at least some females detected are gravid within the population as evidence of reproduction potential. Medium 6–12 months: Reproduction Within 12-month post-release, at least 10% gravid females are detected, and newborn individuals are detected (evidence of recruitment).	Whilst finding gravid females and juveniles is evidence of breeding success, it only demonstrates they individuals can reproduce and is not enough to demonstrate project success (Germano & Bishop, 2009). This result, however, can be considered a partial success because a self-sustaining population is only possible if released individuals reproduce and there is successful recruitment of those reproductive attempts. Thus, our success criteria consist of (1) short-term success – evidence of gravid females within 6 months post-release and (2) medium-term success (6–12 months) – evidence of new juveniles in the population.
Medium 6–12 months: Habitat suitability Within 12 months determine habitat preferences within the reintroduction site for both species.	Habitat quality has long been identified as the primary reason underpinning reintroduction success. Habitat quality constitutes all aspects of the environment (i.e. biotic and abiotic) including predators and habitat characteristics such as vegetation or ground cover. There is little literature on what constitutes suitable habitat for both species, thus, determining the habitat preferences of both species is important. We consider this criterion separate as determining habitat preferences will not successarily determine success/failure; however, this criterion is important for improving long-term management.
Medium 6–18 months: Survival estimates Obtain baseline annual survival rates	Estimates of annual survival are critical for evaluating the probability of short and long-term persistence. Thus, within 6–18 months post-release baseline annual survival estimates are obtained.
Medium 12–18 months: Evidence of population growth: $\lambda > 1$ Based on time to sexual maturity ($\sim$11 months) estimated from captive breeding, we would expect to see evidence of population growth within 12–18 months of release.	A reintroduction project is successful when a self-sustaining wild population is reached or when a population persists. Population viability analyses provide the most objective way to predict long-term persistence of any reintroduced population. In practice, population growth is measured by the growth rate (λ) (which incorporates survival, reproductive success and potentially immigration). Thus, our criterion for success includes short and long-term goals. The short-term goal is to observe population growth within 12–18 months.
Long 3+ years: Self-sustaining population.	The long-term objective is to obtain long-term population growth (λ) $>$ 1.

native tree planting and ongoing management of invasive species such as feral cats (*Felis catus*), black rats (*Rattus rattus*), yellow crazy ants (*Anoplolepis gracilipes*) and the common house gecko (*Hemidactylus frenatus*). Some management of these species continued throughout the study.

To address the primary threats responsible for reptile declines, specifically *L. capucinus* and *S. subspinipes*, a 1 m high electrified aluminium fence was erected around the 2600 m^2 site prior to the release described here. The fence aimed to exclude these predators and restrict post-release dispersal of the arboreal *L. listeri*. Additionally, poison baiting was carried out across the entire site for 3 months prior to the release of *C. egeriae* to ensure eradication of *S. subspinipes* (see Appendix S1, Table S1). Furthermore, to address concerns raised by the failed first (2017) trial (see Emery, 2021), we undertook major habitat enhancements within the site prior to the second trial. These included adding *c*. 10 tonnes of rock, 20 tonnes of logs and branches to the enclosure, as well as scattered artificial habitat (wooden pallets and roofing tiles).

Reintroductions

Cryptoblepharus egeriae

In August 2018, 170 *C. egeriae* were released within the exclosure over a 3-day period. A mixed cohort of *C. egeriae* ($\sim$51% female) was sourced from the captive breeding population on Christmas Island (see Appendix S1, Table S2), and all individuals were weighed in grams (to two decimal places), measured (snout-vent length; SVL in mm) and given a unique toe-clip combination for identification for mark-recapture. Finally, prior to the release, individuals were screened for any signs of ill-health, particularly infections by

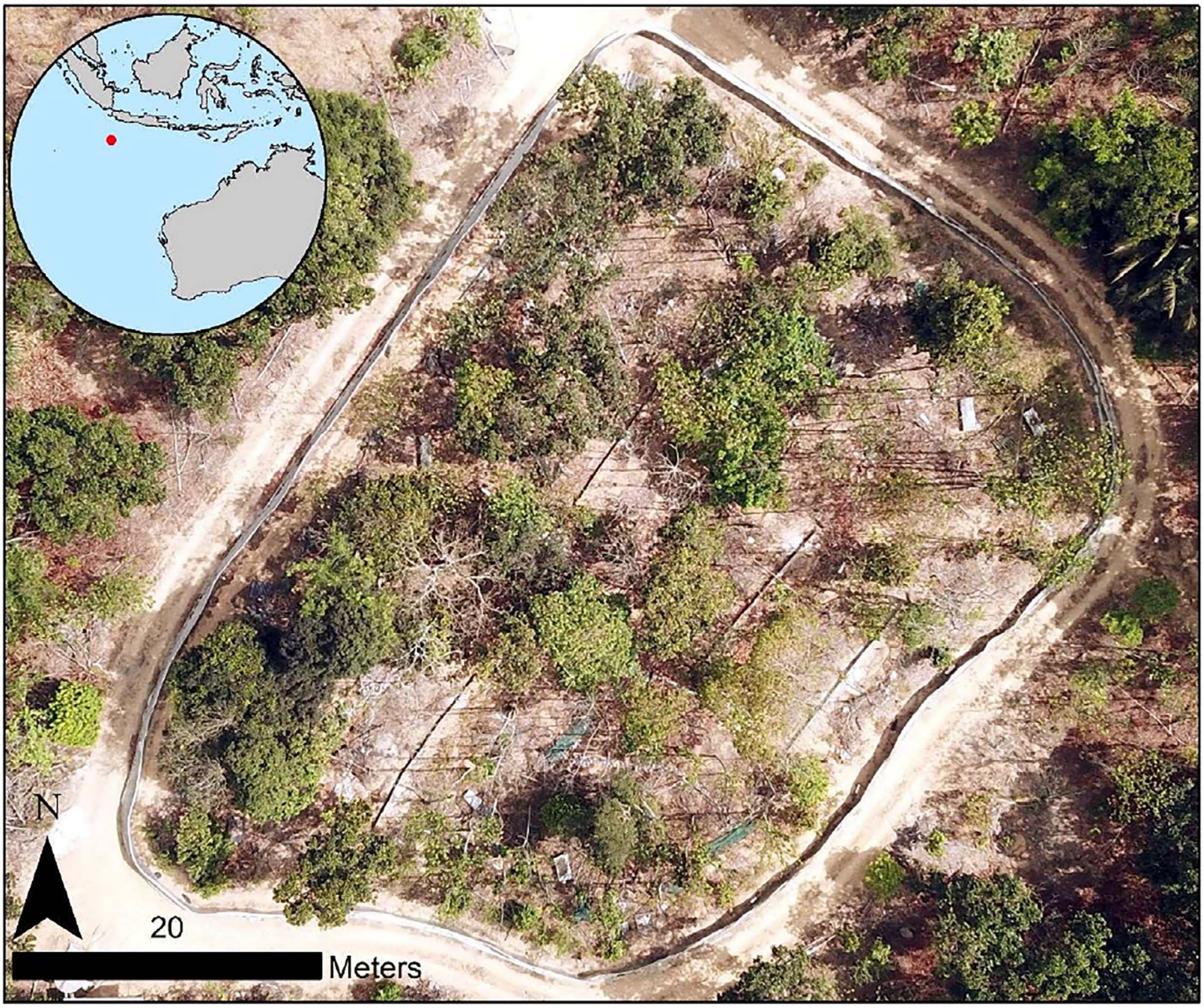

Figure 1 Aerial view of the 2600 m^2 reintroduction site for the blue-tailed skink and Lister's gecko on Christmas Island (inset shows the location of Christmas Island relative to Indonesia and Australia). This site is bounded by a 1 m high galvanized metal fence to exclude introduced predators. Artificial habitat (tin and timber piles) added to enhance habitat suitability can be seen scattered throughout the site.

Enterococcus spp., which had caused significant mortality in the captive population (Rose *et al*., 2017; Agius *et al*., 2021). Animals were released in the afternoon to allow them time to find retreat sites.

Lepidodactylus listeri

In February 2019, 160 *L. listeri* were released into the same reintroduction site over a 2-day period. As with *C. egeriae*, a mixed cohort was sourced from the captive breeding population on Christmas Island (see Appendix S1, Table S2), and all individuals were weighed (in grams), measured (snout-vent length; SVL in mm) and assessed for health indicators. Animals were individually marked with a unique Visual Implant Elastomer (VIE) combination injected into the ventral surface of their legs (Northwest Marine Technology, Inc., Shaw Island, WA, USA). As *L. listeri* is nocturnal, animals were released in the early evening. At the time of release, the reintroduction site was occupied by *C. egeriae* arising from the 2018 reintroduction. The decision to use a single site for both species was based on costs of establishing the exclosure and on evidence of co-habitation of the two species prior to their decline in the wild.

Post-release monitoring

Population size and survival

We hand-captured *C. egeriae* within the translocation site ~1-month post-release (September 2018), 6 months post-release (February 2019), 10 months post-release (June 2019) and 15 months post-release (November 2019) for 5–6 consecutive days. For *L. listeri*, we hand-captured individuals 2 months post-release (April 2019) and 10 months post-release (December 2019) for 5 consecutive days. All capture sessions followed a robust design (see Table S3 in

Appendix S1). To ensure sufficient and representative coverage across the site, quadrats (*c*. 25 m by 25 m each) were systematically searched for 1 h per day. Searches occurred between 07:00–11:00 AM (*C. egeriae*) or 18:30–22:30 PM (*L. listeri*), with two people per session. Searches for both species involved looking for active individuals and carefully rolling rocks, logs and artificial refuges (e.g. roofing tiles). Captured individuals were transported to the captive breeding facility, where they were weighed and measured before being released back into the site on the same day. Newly recruited individuals were given a unique toe-clip combination (*C. egeriae*) or VIE tag (*L. listeri*) and also released back into the site on the same day. Population size and survival was then estimated using a Bayesian mark-recapture model (see data analysis below).

The barrier fence around the site was designed to keep introduced predators out of the site and retain released lizards within it. However, we considered it possible that *L. listeri* could climb the barrier fence, and so following their release, we haphazardly searched surrounding habitat up to 10 m beyond the site. Given the absence of *L. listeri* from the wild prior to this study, any individuals recorded outside the release site must have been founders or their progeny. We attempted to catch any *L. listeri* individuals seen in such searches, and when successful we returned them to the release site.

Habitat use

To examine habitat use by *C. egeriae* and *L. listeri* within the reintroduction site, we described the characteristics of sites utilized by each species. We recorded 10 microhabitat characteristics (see Table S4 in Appendix S1) within a 1 m^2 area centred on each sighting of *C. egeriae* and *L. listeri* following searches along 5 transects spaced 10 m apart across the site. Four transects were 40 m long, and the fifth transect was 35 m long. For *C. egeriae*, habitat variables were collected for every third sighting, whilst they were collected for every sighting of *L. listeri*. To assess if *C. egeriae* and *L. listeri* were selecting microhabitats non-randomly, we also generated 160 random 1 m^2 habitat quadrats within the reintroduction site. Using a random number generator, we determined (1) the length along the transect (0–40 m), (2) left or right of the transect and (3) the perpendicular distance from the transect (0–5 m). Principal components analyses and linear models (see statistical analyses) were used to determine if the species selected habitat variables based on their availability.

Statistical analyses

Body condition

To assess the post-release trend in body condition of *C. egeriae* and *L. listeri*, we calculated body condition as the residuals from a linear regression between the logarithms of body mass and SVL. For the immediate post-release effect, we focused on individuals measured both at release and one-month post-release, excluding those with tail loss, for both species. Linear mixed-effect models (LMMs) were employed, considering Session, Sex, the interaction between these two variables, and individual ID as a random effect. Furthermore, we examined changes in body condition over time for both species: 1-, 6-, 9- and 15-months post-release for *C. egeriae* and 1- and 10-month post-release for *L. listeri*. In the case of *C. egeriae*, we included an additional factor, 'founder,' to evaluate potential differences in body condition between founder and wild-born individuals. To account for non-linear patterns, a quadratic term for time was included based on visual inspection of the data. All models were fitted using the statistical program R version 4.3 (R Core Team, 2023) with the *glmmtmb* package (Brooks *et al*., 2017). We assessed the assumptions of normality for all models using the *DHARMa* package.

Post-release survival and population size

We fit Bayesian mark-recapture models to estimate mortality rates and population sizes using nimble 1.0.1 (De Valpine *et al*., 2017) in R 4.3.1 (R Core Team, 2023) using default Markov chain Monte Carlo (MCMC) algorithms. We used weakly informative priors for all parameters (Appendix S2, Table S1). We assessed MCMC performance through visual inspection of chain histories and Gelman-Rubin statistics. We ran 4 chains for 10 000 iterations after discarding the first 1000 as burn-in. We report parameters with posterior modes and 95% highest posterior density intervals (HPDI).

Brief model description

We built continuous-time robust design multistate Jolly–Seber models (Jolly, 1965; Seber, 1965; Schwarz, Schweigert, & Arnason, 1993; Kéry & Schaub, 2012) to investigate life-stage specific mortality rates of *C. egeriae* and *L. listeri* and to explore effects of sex (for *C. egeriae* and *L. listeri*) and founder status (*C. egeriae* only). For *C. egeriae*, we modelled 5 primary occasions $t \in \{1, 2, \ldots, T = 5\}$ with 5–6 secondary surveys $k \in \{1, 2, \ldots, K_t\}$ per primary and augmented our 693 observed individuals with 800 pseudo-individuals $i \in \{1, 2, \ldots, M = 693 + 800\}$. For *L. listeri*, we modelled $t \in \{1, 2, 3\}$ primary occasions with $k \in \{6, 7\}$ secondary surveys and augmented 160 observed individuals 50 pseudo-individuals $i \in \{1, 2, \ldots, M = 160 + 50\}$. Both data augmentations were sufficient with the entire posterior distributions for the superpopulation being less than M (Royle & Dorazio, 2012). We assessed goodness-of-fit through posterior predictive checks (PPCs) by calculating χ^2 statistics for the number of juvenile and adult captures for each secondary occasion and calculating Bayesian p-values (BPVs) for both life stages separately. Our models included four ecological states z: (1) not yet entered, (2) alive as juvenile, (3) alive as adult, (4) and dead. Because the translocations of individuals only occurred on the first occasion, we modelled the ecological and observation processes for all primaries after the first. We parameterised the state-specific mortality rates and maturation rates in continuous-time to account for the unequal time intervals between primaries (ranging from 1–6 months) (Glennie *et al*., 2022). See

Appendix S2 for full model details and find reproducible code at github.com/mhollanders/ci-skinks.

Habitat use

To investigate fine-scale habitat use by *C. egeriae* and *L. listeri*, we performed a principal components analysis (PCA) on the habitat variables shown in Table 3. The PCA combined habitat variables into fewer factors that were weighted based on their importance. This generated Principal Components (PC's) with a loading for each habitat value between −1.0 and +1.0. We then used linear models to test if occupied versus random habitat differed on each PC that had an eigenvalue >1 and used 0.50 as the minimum loading value for a habitat variable when interpreting each PC. We then used linear models to test if used versus random habitat differed on each PC. We performed the PCA in R using the *factoextra* package (Kassambara & Mundt, 2020) and then used the *visreg* package (Breheny & Burchett, 2017) to generate partial residual plots.

Results

Body condition

The best model for *C. egeriae* comparing condition in individuals pre- and post-release found that there was an effect of time and sex (Table 2). We detected a mean 3.61% (95% CI: −0.05 to 0.02) reduction in body condition at one-month post-release in 31 recaptured *C. egeriae*; however, there was no significant difference between sexes (Table 2, Figure S1 in Appendix S1). 93% (29/31) of recaptured individuals had a lower weight at 1-month post-release than at the time of release.

When investigating longer-term trends in body condition, the best model found a strong interaction between founder and session with an additive effect of sex (Table S5 in Appendix S1). Body condition decreased until 9 months post-release but increased by 15-months post-release ($n = 466$, Fig. 2). Males lost significantly more body condition than females and juveniles (Table S5 in Appendix S1).

The best model comparing individuals pre- and one-month post-release for *L. listeri* included the factor time (Table 2). We detected a mean loss of 5% (95% CI: −0.08 to −0.01) in body condition of 12 recaptured *L. listeri* one-month post-release (Figure S1 in Appendix S1). 92% (11/12) of recaptured individuals had a lower weight 1-month post-release than at the time of release. When looking at longer term trends, *L. listeri* increased body condition 2–10 months post-release ($n = 118$; Fig. 2; Table S5 in Appendix S1).

Abundance and survival of *C. egeriae*

We made 1095 captures (574 juveniles, 521 adults) of 693 individual skinks (523 individuals excluding translocated founders). Of the 170 *C. egeriae* released, we recaptured 106 individuals (62%) one-month post-release. Across all individuals, 155 were recaptured once, 45 were recaptured twice, 20 were recaptured three times, and 5 were recaptured during all four post-translocation capture sessions. The number of *C. egeriae* observed increased from 106 at one-month post-release to 337 at 15 months post-release. Population sizes derived from latent ecological states revealed a 5-fold estimated population increase from the initial 170 to 1025 (95% CI: 903–1144) (Fig. 3). The Bayesian *p*-values were good for juveniles (0.343) and adults (0.464), suggesting good model fit. Our modelling revealed that in the absence of life-stage specific random survey variation (compared to no random survey effects or survey effects shared across life stages) the model fit was poor, with Bayesian *p*-values close to 0.

The monthly per-female recruitment rate was estimated to be 0.382 (95% HPDI: 0.218–0.549) (Table S1 in Appendix S2). Monthly mortality rates of juveniles (0.068, 95% HPDI: 0.022–0.117) and adults (0.081 95% HPDI: 0.04–0.126) did not differ meaningfully, and correspond to an average annual survival probability of 0.404 (95% HPDI: 0.278–0.562) (Table S1 in Appendix S2). Males had lower mortality rates than females (log hazard change −0.305, 95% HPDI: −0.726 to 0.134) and founder animals had higher mortality rates than non-founders (log hazard change −0.024, 95% HPDI: −0.502 to 0.539) (Figure S1 in Appendix S2). Adult capture probabilities were estimated to be 0.065 (95% HPDI: 0.045–0.089), which was 0.006 (95% HPDI: −0.015 to 0.031) higher than for juveniles (0.059, 95% HPDI: 0.05–0.069), with minimal variation between surveys for both juveniles (SD of random effects: 0.275, 95% HPDI: 0.106–0.51) and adults (SD of random effects 0.521, 95% HPDI: 0.344–0.761) (Figure S1 and Table S2 in Appendix S2). Capture probabilities were higher for founders

Table 2 Results of linear mixed effects models investigating the effects of translocation on body condition 1 month post-release. The interactions between session and sex were not significant and was removed from final models

	Estimate ± SE	95% CI	d.f.	z value	*P* value
2018: *C. egeriae* 1-month post-release, $n = 32$					
Session	−0.03 ± 0.006	−0.04 to −0.02	31	−5.69	<0.000
Sex[a]					
Male	−0.03 ± 0.008	−0.05 to −0.02	29	−4.17	<0.000
Unknown	−0.02 ± 0.008	−0.04 to −0.01	29	−3.37	<0.000
2019: *L. listeri* 1 month post-release, $n = 12$					
Session	−0.05 ± 0.01	−0.07 to −0.02	11	−3.519	0.001

[a] Female is the reference level.

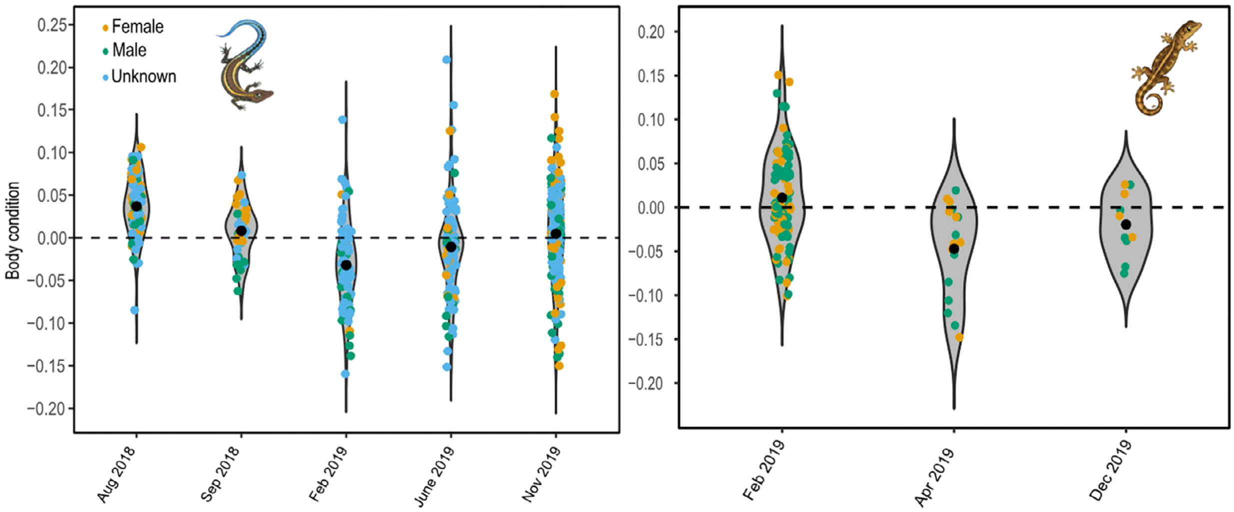

Figure 2 Violin plots of % variation in body condition relative to release body condition of *C. egeriae* and *L. listeri* over 15- and 10-month post-release, respectively. The middle black dot represents the median value, the grey-shaded areas span 95% of the data and the coloured dots represent observed values. The first date in each plot represents the release date.

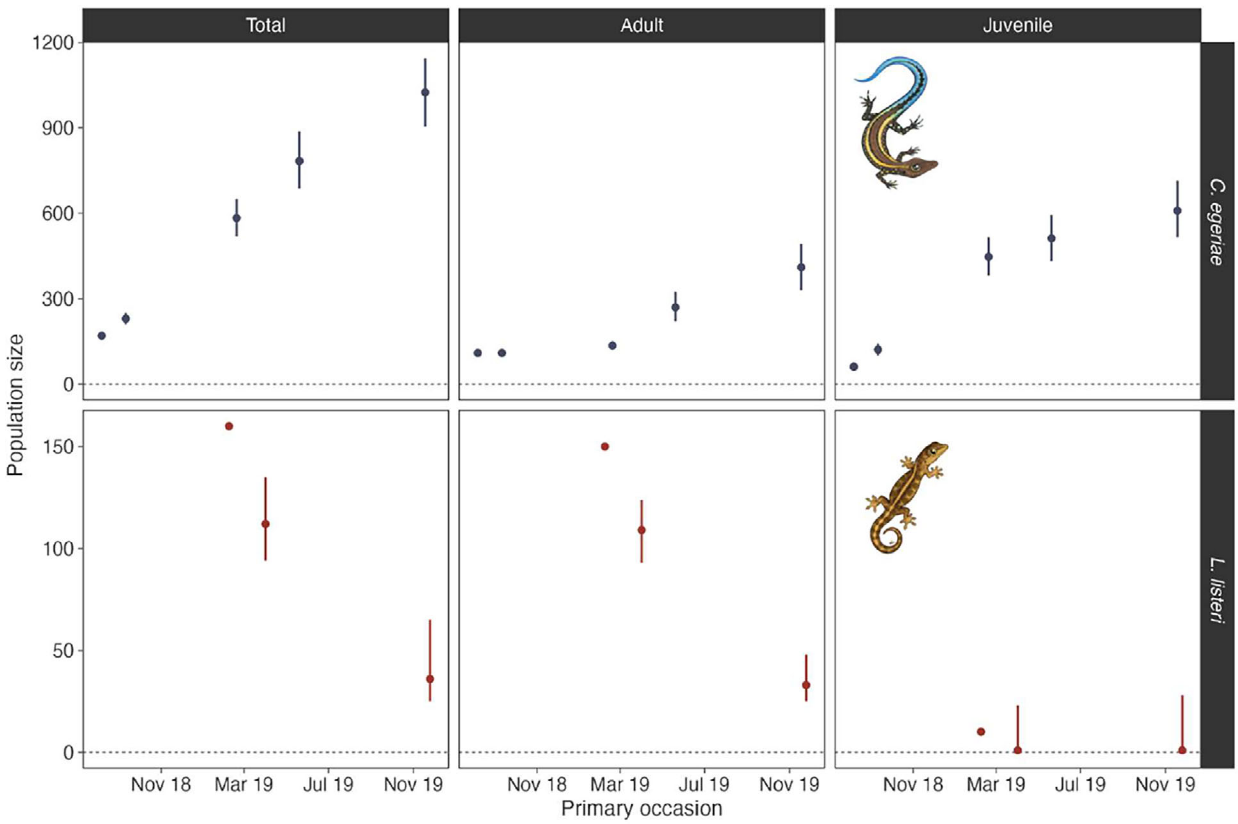

Figure 3 Posterior distributions (with medians and 95% HPDI) of total, adult and juvenile population sizes of *Cryptoblepharus egeriae* and *Lepidodactylus listeri* per primary occasion (note different start dates for each species). Circles without error bars indicate initial number of released individuals.

(log odds change 0.985, 95% HPDI: 0.671–1.296) (Table S1 and Figure S1 in Appendix S2).

Abundance and survival of *L. listeri*

Overall, we made 96 captures (7 juveniles, 89 adults) of 49 individuals. We only captured four individuals that were not part of the initial release. Among the 160 individuals we released, we recaptured 33 individuals at 2 months post-release (20%) and 24 individuals (15%) at 10 months post-release. Estimated population sizes for the two primary occasions showed a decline in adults and juveniles from the initial 160 released to 36 (95% CI: 24–62) at 10-months post-release (Fig. 3). The fit for this model was adequate, with Bayesian p-values of 0.273 and 0.011 for juveniles and adults, respectively.

Monthly per-female recruit rates were estimated to be low at 0.004 (95% HPDI: 0–0.178) (Table S2 in Appendix S2). Juvenile (0.234, 95% HPDI: 0–0.895) and adult mortality hazard rates (0.175, 95% HPDI: 0.122–0.231) were high and corresponded to an average annual survival probability of 0.085 (95% HPDI: 0–0.315). Juvenile and adult capture probabilities were similar with an average detection probability of 0.086 (95% HPDI: 0.038–0.199), with limited variation between surveys (SD of random effects 0.487, 95% HPDI: 0.004–0.862). Sex effects on mortality rates and detection probabilities were inconclusive with large uncertainty intervals (Table S2 in Appendix S2). The fit for this model was adequate, with Bayesian P-values of 0.407 and 0.419 for juveniles and adults, respectively.

Habitat use

For the assessment of habitat use by *C. egeriae*, the PCA incorporated eight fine-scale habitat variables that resulted in four PCs with eigenvalues >1 that together explained 65% of the habitat variance (Table S6 in Appendix S1). Used and available habitat differed significantly for PC1 ($F = 85.36$, d.f. = 1,469, $P < 0.001$), PC3 ($F = 11.73$, d.f. = 1,469, $P < 0.001$) and PC4 ($F = 9.85$, d.f. = 1,469, $P = 0.001$), but not for PC2 ($F = 0.565$, d.f. = 1,469, $P = 0.453$). PC1 and PC4 showed that sites with *C. egeriae* had higher values on these axes than available locations, corresponding to higher log cover, number of logs and vegetation cover (Fig. 4a, c). PC3 showed that sites with *C. egeriae* had lower values on this axis than available locations corresponding to higher rock cover (Fig. 4b).

For *L. listeri* the PCA incorporated eight fine-scale habitat variables that resulted in four PCs with eigenvalues >1 that together explained 73% of the variance (Table 3). Used and available habitat differed significantly for PC1 ($F = 10.35$, d.f. = 1,238, $P < 0.001$), PC2 ($F = 13$, d.f. = 1,238, $P < 0.001$) and PC4 ($F = 36.57$, d.f. = 1,238, $P < 0.001$), but not PC3 ($F = 1.946$, d.f. = 1,238, $P = 0.164$). PC1 and PC4 showed that sites with *L. listeri* had higher values on these axes than available locations corresponding to more log cover and rock cover (Figure S2a–c in Appendix S1). PC2 showed that sites with *L. listeri* had lower values than available locations on this axis (Figure S2b in Appendix S1), corresponding to a greater cover of leaf litter.

Assessment against success criteria

Body condition in both species decreased by only *c.* 5% 1–-2 months post-release and thus met our criteria for success. We detected both short- and medium-term success for reproduction in both species. For short-term and medium-term survival and population growth, only *C. egeriae* met both criteria for success (Table 4). Finally, we assessed habitat preferences for both species, and our results indicate that both species showed some significant non-random habitat selection for logs and rocks within the reintroduction site. Table 4 provides further detail on these conclusions.

Discussion

The primary aim of most fauna reintroduction programs is to establish self-sustaining populations as a mechanism to conserve or recover the species (Armstrong & Seddon, 2008). However, the evaluation of success depends on species' life history traits, requiring assessments over periods ranging from 5 to 20 years for long-lived species (Bertolero & Oro, 2009; Moseby *et al.*, 2011). In our study, we focused on reintroduction trials of the only two reptile species currently recognized as Extinct in the Wild, and we successfully implemented monitoring protocols designed to evaluate progress relative to *a priori* success criteria. Importantly, we found that for the first time, both species can survive and reproduce in a semi-wild environment, despite being restricted to captivity for nearly a decade. We demonstrated the utility of short- and medium-term criteria for prioritizing post-release monitoring and evaluating reintroduction success but acknowledge they may not be accurate predictors of the long-term establishment for either species.

Criteria for success

Our assessment of the criteria revealed strikingly different outcomes for each species, particularly in their population trajectories post-release. *Cryptoblepherus egeriae* exhibited sustained population growth during the 15-month post-release period, with the capture of many site-born juveniles from two generations, indicating successful progress towards the long-term goal of a self-sustaining population (Table 4). In contrast, *L. listeri* experienced a significant population decline despite some reproductive success, indicating a limited likelihood of achieving a self-sustaining population (Table 4). Additionally, both species displayed a preference for habitat features that were relatively limited within the reintroduction site, such as log and rock cover, whilst avoiding areas with low ground cover. Based on our short- and medium-term criteria, the reintroduction trial of *C. egeriae* can be considered successful over the period of monitoring described here. However, whilst *L. listeri* achieved short-term success for body condition and reproduction, medium-term success in population growth was not realized.

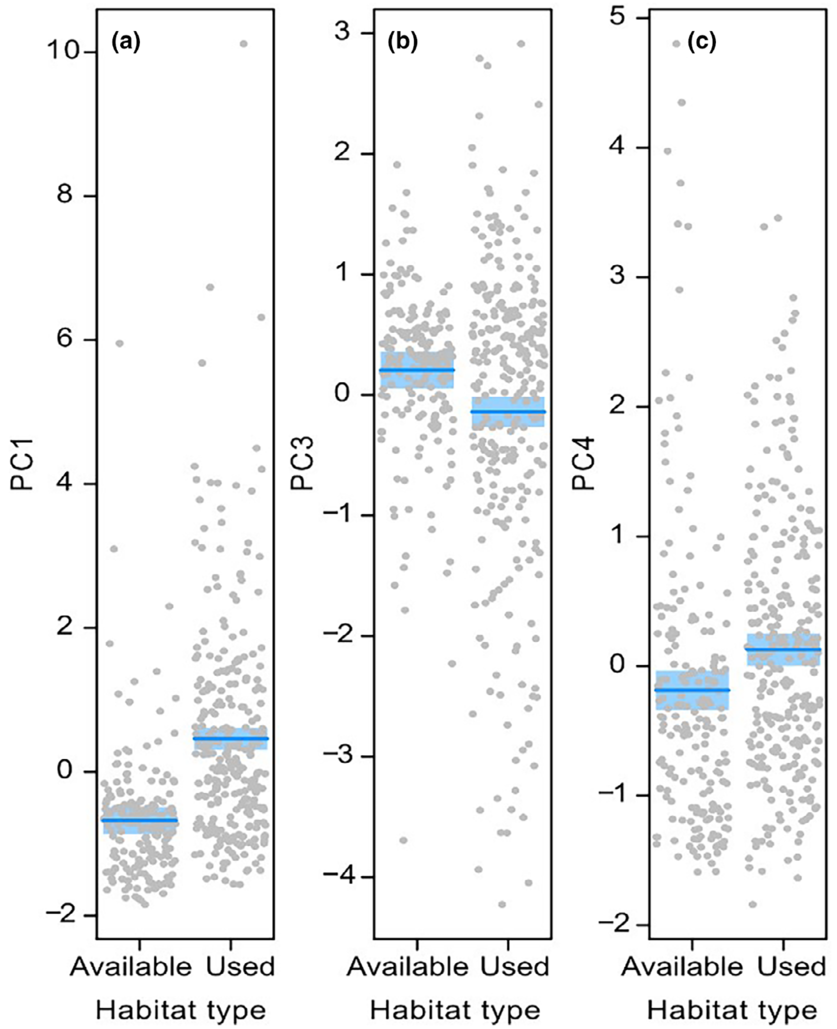

Figure 4 Partial residual plots with 95% confidence bands showing values from a principal components analysis for PC1 (a), PC3 (b) and PC4 (c) in habitat available to and used by *Cryptoblepharus egeriae*. Habitat variables included in the principal components and their loading values are presented in Table S6 in Appendix S1.

Table 3 Eigenvalues and loading values from a principal component's analysis for the habitat characteristics within the reintroduction site for *Lepidodactylus listeri*

Eigen and loading values	PC1	PC2	PC3	PC4
Eigenvalues	1.83	1.74	1.21	1.06
Variation explained	22.87	21.81	15.21	13.36
Loading values				
Log cover (%)	0.60	0.58	−0.06	0.35
Bare ground cover (%)	−0.76	0.43	−0.25	0.26
Leaf litter cover (%)	0.48	−0.75	−0.34	0.08
Branch cover (%)	0.24	0.17	−0.40	−0.51
Vegetation cover (%)	−0.12	−0.11	0.77	0.24
Rock cover (%)	0.18	0.35	0.45	−0.69
Number of logs	0.61	0.61	−0.03	0.25
Canopy cover (%)	0.44	−0.35	0.30	0.13

Body condition

In both species, body condition significantly decreased, albeit only marginally, in the first-month after reintroduction. Whilst this decrease could be attributed to the stress of release (e.g. handling, transport), it is unlikely as individuals experienced similar handling during captivity. Instead, the decline in body condition is more likely an artifact of high body condition in captivity (e.g. Snyder *et al.*, 1996; Connolly & Cree, 2008). Animals in captivity had access to abundant food resources (e.g. being provided with food 3–4 times a week) and were likely less active due to being in confined spaces and not having to hunt and find refugia. Consequently, weight loss following release is expected due to the energetic demands of competition for food, breeding behaviours (e.g. male aggression), increased roaming movements and predator avoidance (e.g. predatory birds that had

Table 4 Comparison of *Cryptoblepharus egeriae* and *Lepidodactylus listeri* reintroduction performance against success criteria

Criteria for success	Result		Conclusion
	C. egeriae	*L. listeri*	
Short (1–2 months): Body condition is maintained or decrease by <10% 1 month after release.	A mean decrease of 4% short-term.	Decreased by 5% short-term	Success
Short (1 month): >50% founder survival in the first-month post-release	62% of founder animals captured 1 month later.	20% of founder animals captured 2 months later.	Success for *C. egeriae* but fail for *L. listeri*
Short (0–6 months): Evidence of reproduction observed in 0–6 months.	One month post-release 46% of females had signs of reproduction (i.e. bite marks) or were gravid.	No females showed signs of reproduction in the first 6 months post-release.	Success for *C. egeriae* but fail for *L. listeri*
Medium (6–12 months): Newborns are detected and join the population each year.	Captured >100 site-born individuals in the first 12 months in at least two generations.	Captured four site-born individuals	Success
Medium (6–12 months): Estimates of survival	Estimated annual survival 48% (95% HPDI: 35–62%)	Estimated annual survival of 10% (95% HPDI: 0–36%)	Success
Medium (6–12 months): Determine habitat preferences	Both *C. egeriae* and *L. listeri* selected non-randomly for areas high in log and rock cover in the reintroduction site. Both species also avoided areas with a high degree of bare ground.		Achieved
Medium (12–18 months): Population growth	We estimated a significant (5-fold) population increase in the 15 months post-release. Captured individuals from at least two generations.	We estimated a significant population decline in the 10 months post-release	Success for *C. egeriae* and fail for *L. listeri*
Long 3+ years: Self-sustaining population: Obtain a population growth rate >1	Not evaluated	Not evaluated	–

access to the site) (Matthews, 2003; Brannelly *et al.*, 2016; Robinson *et al.*, 2021). Our data indicate that the loss of body condition primarily occurred during the initial establishment phase, as both *C. egeriae* and *L. listeri* exhibited increasing body condition by 15 and 10 months, respectively (Figure 2). This suggests that food availability was adequate for both species. Furthermore, for *C. egeriae*, the initial decline in body condition had no long-term effects, considering high post-release survival and subsequent population growth rate. This finding aligns with (Hare *et al.*, 2012, 2020), which showed that body condition in captive lizards (Suter's skinks – *Oligosoma suteri*) had minimal impact on survival, and indeed, larger skinks with lower body condition after 12 months had better post-release survival. One limitation of this criterion in our study is that it only considers recaptured individuals: individuals not recaptured (that may have died) may have had more loss of body condition.

Apparent survival and growth

In our study, *C. egeriae* met our benchmark of achieving at least 60% survival in the first-month post-release, which coupled with a high reproduction rate, led to rapid population growth. This survival rate greatly exceeded that of the initial (2017) unsuccessful reintroduction trial for *C. egeriae*, for which short-term survival was below 30% (Emery, 2021). Despite the initial high survival for *C. egeriae*, we found strong evidence of a founder effect in *C. egeriae* whereby founder animals had significantly lower survival than their wild conspecifics (Table S2 in Appendix S2). In contrast, the *L. listeri* trial featured a low recapture rate of *c*. 20% of founders after 2 months, followed by rapid population decline, resembling the first *C. egeriae* reintroduction attempt. Release costs on individuals prior to them becoming familiar with their new environments has been reported in many reintroduction programmes (Stamps & Swaisgood, 2007; Armstrong & Seddon, 2008; Parker *et al.*, 2012) and can stem from the stress of release and adapting to new conditions (foraging, finding refugia, etc). Thus, our results suggest that high survival in the establishment phase is critical for both species, which aligns with other findings in reptile reintroductions (Germano & Bishop, 2009; McCoy *et al.*, 2014; Fitzgerald *et al.*, 2015).

As with captive populations, male *C. egeriae* in our study showed higher apparent survival compared to females (Figure S1 and Table S1 in Appendix S2), and adults exhibited higher survival than juveniles, though not significantly so (Figure S1 and Table S1 in Appendix S2, Christmas Island National Park, unpublished data). The reasons for these differences remain unclear; however, in captivity, there is considerable male-induced mortality on females during the breeding season. Due to high uncertainty, we were unable to determine if there were sex differences in *L. listeri* survival; however, under captive conditions, there is no evidence of this occurring.

The results underlining the low apparent survival for *L. listeri* are inconclusive, as we were unable to determine whether low post-release survival was due to high mortality or dispersal out of the exclosure (and hence beyond our monitoring effort). Despite the presence of an electrified fence intended to prevent dispersal, we opportunistically detected (and returned) over 30 *L. listeri* (*c*. 20% of the number of founders) outside the reintroduction site in the first-month post-release, demonstrating the ineffectiveness of the barrier for preventing emigration from the site. Although we surveyed the area immediately adjacent to the reintroduction site at least once each fortnight, we did not detect any *L. listeri* outside the site thereafter, suggesting that their dispersal may have been limited to the immediate post-release period, or that over time they dispersed beyond our search area, or that they died after initial dispersal. Notably, a review of hyperdispersal in translocated animals (Bilby & Moseby, 2023) found that in published reptile studies, between 5–25% of individuals were observed to hyperdisperse from their release site, aligning with our finding of ~20%. Captive animals may disperse immediately after release due to perceiving the release site as unsuitable and seeking conditions resembling those in captivity based on positive associations (Stamps & Swaisgood, 2007). In our study, the captive population of *L. listeri* was raised in large canvas tents ($1.8 \times 1.8 \times 1.8$ m) containing branches, bark and artificial retreats, potentially contributing to high post-release dispersal due to the limited amount of such features in the reintroduction habitat. Whilst we could not differentiate between mortality and emigration, barriers that better restrict dispersal may improve outcomes during the establishment phase of future *L. listeri* reintroductions, as they have done in other studies (Ebrahimi & Bull, 2013; Knox & Monks, 2014; Knox *et al*., 2017).

Habitat use by *C. egeriae* and *L. listeri*

We observed that *C. egeriae* preferred structurally complex areas and avoiding areas with low ground cover (Fig. 4, Table S6 in Appendix S1). Although this is the first study to examine microhabitat selection in *C. egeriae*, previous observations before their extirpation frequently found this species on tree trunks, limestone pinnacles and on ornamental trees, fences and houses in urban areas (Cogger, Sadlier, & Cameron, 1983; James, 2007). Generally, *C. egeriae* are considered to be a semi-arboreal to arboreal species, as demonstrated by subsequent translocations to the Cocos (Keeling) Islands, where they primarily utilize trees and shrubs (Schubert, 2020). The lack of preference in our study for trees may be attributed to the young age of the trees in the reintroduction site, which lacked the structural elements (e.g. exfoliating bark and hollows) that older trees offer for predator avoidance and refuge. However, this species appears to exhibit a degree of adaptability and generalist behaviour, as rock and log cover seem to provide suitable habitat for meeting their thermoregulatory needs, and for foraging and shelter.

As for *C. egeriae*, logs and rocks emerged as the most important habitat characteristics for *L. listeri*, a surprising result given that *L. listeri* is arboreal and frequently occurred on tree trunks and branches several meters above the ground (Cogger, Sadlier, & Cameron, 1983). It is plausible that logs and rocks serve as critical refuges during the day, especially when suitable arboreal refuges and habitats are limited. Since the reintroduction site was located within a mining restoration area, the relatively young trees may have lacked the structural complexity preferred by *L. listeri*. A study on the black-headed dwarf chameleon (*Bradypodion melanocephalum*) in South Africa reported similar findings, demonstrating that a translocated population only endured in areas where sufficient time had passed for the restoration of native vegetation (Armstrong, 2008). Furthermore, it is possible that the prior occupation of our release site by *C. egeriae* may have usurped or diminished suitable habitat for *L. listeri* or otherwise reduced prospects for its retention. Further studies, including release of *L. listeri* to sites without *C. egeriae*, are warranted. Subsequent habitat distribution modelling within the site indicated that significant portions of the reintroduction area are unsuitable for *L. listeri*, which may have contributed to high mortality or dispersal (Emery, 2021). Consequently, our observations of *L. listeri* near refuge sites may be a consequence of the initial high dispersal observed, emphasizing the need for future trials that manipulate these factors.

Conclusions

Our study on the trial reintroductions of two globally Extinct in the Wild reptile species revealed their ability to survive and reproduce during the initial establishment phase of the reintroductions (i.e. 10–15 months post-release). Particularly promising was *C. egeriae's* rapid population growth under suitable conditions, as captive animals typically exhibit lower performance compared to their wild counterparts (Snyder *et al*., 1996; Connolly & Cree, 2008; Hare *et al*., 2020). Global adoption of short- and medium-term criteria for assessing success in reptile reintroductions is now common (e.g. Bertolero & Oro, 2009; McCoy *et al*., 2014; Miller, Bell, & Germano, 2014), but there is less imperative to continue long-term monitoring. However, the need for ongoing monitoring became particularly evident in our study, as a decline was detected in the *C. egeriae* population after the initial success described here.

By early 2021, a marked population decline occurred in *C. egeriae*, accompanied by the intrusion of several wolf snakes into the exclosure, despite the barrier fence remaining intact. Extensive effort was immediately made to remove the snakes and whilst some snakes were captured and removed, the population of *C. egeriae* continued to dwindle. By *c*. 31 months, managers decided to end the trial and to return the remaining *C. egeriae* to captivity. This decision was driven by an emerging consensus that wolf snakes had caused the extirpation of native Christmas Island reptiles in the wild (Emery *et al*., 2021a, 2021b) and that there was a risk that the reintroduced population of *C. egeriae* might also be extirpated if the decision was delayed. Ultimately, only 170 individuals were captured from a population that had reached close to 1000 individuals.

The failures of these reintroductions highlight the concern that despite achieving short- and medium-term objectives, long-term success is not guaranteed. Setting short-term and medium criteria has been instrumental in developing monitoring methodologies for subsequent *C. egeriae* and *L. listeri* reintroductions, and these methods remain crucial for enhancing the likelihood of their long-term persistence in enclosures. Even in failure, the use of short-term objectives has provided valuable insights to inform future reintroductions of two Extinct in the Wild species and can be incorporated in translocation programs for other short-lived reptiles, such as the Nactus gecko from Mauritius.

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Author contributions

JP, NM, JW, BT, HC and LV conceived the study. JP & LV developed methodology. JP, BT, KR undertook the fieldwork. JP & MH analysed the data, JP led writing of the manuscript with contributions from all authors.

Ethics statement

This research was approved under the University of Western Australia's animal ethics permit number R/3/100/1542 and permits from Parks Australia, permit number CINP_2017_07. The authors declare there is no conflict of interest.

Data availability statement

All data used in the body condition and habitat analyses will be made freely available on the public repository Figshare, https://doi.org/10.6084/m9.figshare.25024685. Survival and population script and associated data are on GitHub (https://github.com/mhollanders/ci-skinks).

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Management actions taken prior to the second *C. egeriae* trial.

Table S2. Demographics of release cohorts for each reintroduction.

Table S3. Four assumptions and their justification for undertaking the robust design for mark-recapture analyses.

Table S4. Microhabitat variables measured within quadrats centred over 180 *C. egeriae*, 49 *L. listeri* and 160 random locations within the soft release site.

Table S5. Results from linear mixed effects models investigating effects of reintroduction on body condition of *C. egeriae* and *L. listeri*.

Table S6. Eigenvalues and loading values from a principal components analysis for the habitat characteristics within the reintroduction site for *C. egeriae*.

Figure S1. Violin plots of release and 1-month post-release body condition for (A) *C. egeriae* reintroduction and (B) *L. listeri*. The middle black dot represents the median value, grey shaded areas span 95% of the data, and coloured dots represent observed values.

Figure S2. Partial residual plots with 95% confidence bands showing values from a principal components analysis for PC1 (a), PC2 (b) and PC4 (c) in habitat available to and used by Habitat variables included in the principal components and their loading values are presented in Table 2 in published manuscript.

Appendix S2. Methods and results for Christmas Island skink analysis.