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RESEARCH ARTICLE

Determinants of successful establishment and post-translocation dispersal of a new population of the critically endangered St. Croix ground lizard (*Ameiva polops*)

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Translocation to areas free of exotic predators, habitat degradation, or disease may be the most viable restoration option for many endangered species. We report on a successful translocation of the critically endangered St. Croix ground lizard, *Ameiva polops*, extirpated from St. Croix, U.S. Virgin Islands, Caribbean, by predation from introduced mongooses (*Herpestes auropunctatus*). We translocated 57 adult *A. polops* from Green Cay to Buck Island in May 2008. We placed 4 females and 3 males each in eight, 100 m^2, enclosures on Buck Island for 71 days, then the enclosures were opened. During the enclosure period, 20 individuals were identified and 32 others were seen. The average number sighted per survey was only 5.28 (range = 2–10). One hatchling was sighted in an enclosure, indicating a translocated female successfully nested. Body condition of the translocated individuals increased significantly by the end of the enclosure period. Population monitoring surveys at 61 sites across Buck Island showed that 5 years after the initial translocation in June 2013, the new population had grown to an estimated 1,473 individuals and occupied 58.9% of the island. We attribute eradication of mongoose, life history of the species, large propagule size, condition of habitat, soft-release, use of adults, interagency collaboration, and systematic assessment as primary factors that facilitated this successful translocation. Our findings provide meaningful insights on factors that enhance the potential for successful translocations, and point to new strategies aimed at restoring populations of endangered reptiles in their native ranges.

Key words: Caribbean, conservation introduction, island restoration, mongoose eradication, occupancy modeling, population, soft-release, translocation

Implications for Practice

- Success of translocation projects can be predicted from four factors: translocation strategy, life history of the species, habitat quality, and monitoring. Correlates to success may be identified a priori, with predictions formulated as to the relative contributions of each factor identified.
- Replicated soft-release enclosures are predicted to work well for many translocation projects, as they did for this species, because they allow individuals to habituate to new surroundings and risks (e.g. escape and predation) are spread among separate enclosures. Enclosures allow for close monitoring and experimentation.
- Population size and dispersal should be monitored beyond the translocation sites to understand patterns of habitat use, dispersal, and population growth.
- Long-term participation of government, nongovernment, and research collaborators is critical for implementation and monitoring.

Introduction

When primary drivers of population extinction are persistent throughout the range of a species, translocation to an area free of those threats may be one of few viable choices for

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conservation of critically endangered species. Conservation introductions (translocation outside the native range; Ewen et al. 2012) may be the only recourse if nonnative predators, disease, habitat degradation, or exploitation remain uncontrolled in the native range. Conservation introductions are also likely to become more common as endemics faced with extinction from climate change are introduced to entirely new ranges (Thomas 2011). Conservation of island endemics provides particularly relevant examples of restoration of ecosystems that incorporate conservation introductions to establish populations in areas free of introduced predators, disease, or agents of habitat degradation. The special cases of islands often require integrative approaches to restoration, including eradication of nonnative predators, habitat management, and ecological monitoring. Thus, a number of actions must be taken to increase the likelihood a conservation introduction will succeed (Armstrong & Seddon 2007; Ewen et al. 2012).

Translocations (either introductions or reintroductions) have succeeded for island endemics in several instances (Towns & Ferreira 2001; Soorae 2011). Among reptiles, translocations of several species of tortoises, snakes, and lizards have been attempted and in many cases were successful. The success rate for reptile translocations globally doubled from 19 to 41% of cases between 1991 and 2007 (Dodd & Seigel 1991; Germano & Bishop 2009). In a recent sample of eight cases, five were successful, three were partially successful, and one failed (Soorae 2011). In several reviews, factors attributed to success include translocation of a large number of propagules, good quality habitat at the translocation site, removing the cause of decline (e.g. predator control), and political cooperation (Griffith et al. 1989; Fischer & Lindenmayer 2000; Germano & Bishop 2009).

The goal of our effort was to establish a new population of the critically endangered St. Croix ground lizard (*Ameiva polops*: Teiidae [Cope 1862]). Considered among the most rare lizards in the world, *A. polops* is endemic to St. Croix, U.S. Virgin Islands (Schwartz & Henderson 1991) and listed as Endangered in the United States and Critically Endangered by IUCN (U.S. Fish & Wildlife Service 1977; Nellis 1996). It was extirpated from the main island of St. Croix by introduced mongooses (*Herpestes auropunctatus*), and the last individual was seen in Fredriksted in 1968 (Philibosian & Ruibal 1971). Fortunately, *A. polops* persisted in small numbers on Green Cay and Protestant Cay (Philibosian & Ruibal 1971; McNair & Coles 2003; McNair & Lombard 2004). Green Cay (5.17 ha) is a U.S. Fish and Wildlife Service (USFWS) National Wildlife Refuge and the only legally protected native habitat of *A. polops*. Protestant Cay (1.2 ha) is entirely developed with a hotel and resort. An introduced population of *A. polops* exists on a dredge-spoil island, Ruth Cay (5.17 ha) (Fig. 1). Ten *A. polops* from Protestant Cay were released onto Ruth Cay in 1990 (Knowles 1990; McNair & Mackay 2005), and an additional lizard from Green Cay was released there in 1995 (Knowles 1996). Recent genetic analyses indicate the Ruth Cay population does not contain alleles from the Green Cay stock (Hurtado et al. 2012).

Considering its small populations, small size of the three cays where it persists, ongoing threats of predation by mongoose, rats, cats, and other nonnative wildlife, and other risks, it was abundantly clear for decades that *A. polops* was in imminent danger of extinction. Fortunately, mongoose never colonized Protestant Cay and Green Cay, which probably would have lead to the extinction of the St. Croix ground lizard. Translocation was the logical and necessary step to ensure persistence of this critically endangered species. *Ameiva polops* was listed as Endangered in 1977 (U.S. Fish & Wildlife Service 1977), and a recovery plan filed in 1984 (U.S. Fish & Wildlife Service 1984) called for establishment of a “self sustaining population (500 or more individuals) on Buck Island.” Finally, in 2007 with NPS project funding, collaboration among federal and territorial agencies, and academic collaborators were in place to accomplish a translocation.

We designed a conservation introduction to Buck Island based on a priori predictions that the largest justifiable propagule size, translocation of adults, and a female-biased sex ratio would enhance the likelihood of success. We designed the translocation as a soft-release strategy (Bright & Morris 1994) with replicated enclosures, and predicted that containing the lizards in enclosures within their new habitat would serve to reduce predation, increase interactions such as mating encounters among individuals, and greatly facilitate monitoring during translocation.

This case provides new and meaningful insights into the principal correlates of a successful translocation and bears important implications for planning of future translocations of lizards. The findings also point to new strategies that can be developed to restore populations of endangered reptiles in their native ranges.

Methods

Species Information and Translocation Site

Like most teiid lizards, *Ameiva polops* is a heliothermic active forager that spends most of its active time in a combination of thermoregulation and foraging for a variety of invertebrates (Meier et al. 1993). Across its three populations, the species uses a variety of habitats ranging from forest leaf litter, to low-lying scrubby vegetation to landscape plantings on Protestant Cay. The Green Cay population is genetically differentiated from the Protestant Cay and Ruth Cay populations, and these populations all exhibit relatively low genetic diversity and very low effective population sizes (Hurtado et al. 2012; Hurtado et al. 2014).

When scientists recognized *A. polops* was at risk of extinction (Philibosian & Ruibal 1971), Buck Island was considered the most appropriate translocation site because the island was not occupied by other teiid lizards and because of suitable habitat (Philibosian & Ruibal 1971). It is much larger (71.2 ha) than the cays where extant populations persist, and the entire island is potential habitat for *A. polops*. In particular, large portions of the western half of Buck Island have good forest cover and abundant leaf litter. Generally, the habitat is composed of forest that allows dappled light through to the ground and creates leaf litter and decaying organic material that supports invertebrate prey. Herbaceous and shrubby vegetation, leaf litter, and woody debris provide refugia for *A. polops*. Despite its proximity to St.

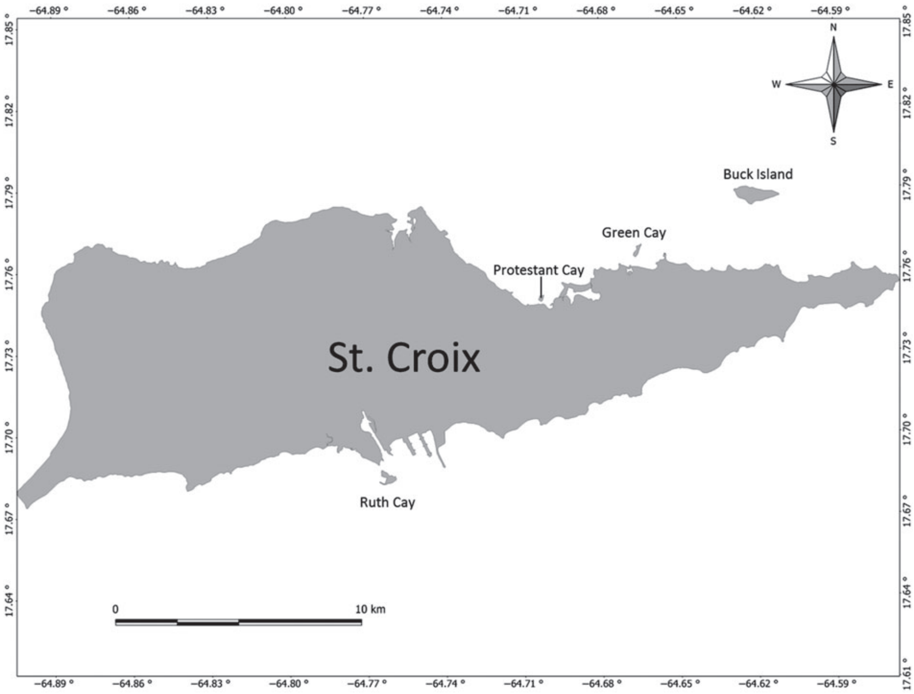

Figure 1. A map of St. Croix, U.S. Virgin Islands, Caribbean. *Ameiva polops* was extirpated from the main island, and persisted on Green Cay and Protestant Cay. A population was established on Ruth Cay in 1990 with individuals from Protestant Cay. We established a population on Buck Island in 2008.

Croix and relatively large size, neither *A. polops* nor any other teiid species has ever been documented to occur on Buck Island. Without fossil evidence, it is impossible to know if a species of ground lizard ever occurred there.

Buck Island is protected by the U.S. National Park Service, and a program to eradicate mongoose and rats, and restore native vegetation has existed for more than 30 years. During the 1970s through the mid-1990s, more than 500 mongoose were trapped and removed from Buck Island, and the island was free of mongoose by 1995 (Z. Hillis-Starr, unpublished data). Roof rats (*Rattus rattus*) were also identified as a potential threat to *A. polops*, and a program to eradicate them was undertaken from 1998 to 2000. Rat eradication was accomplished by positioning 428 elevated bait stations in an island-wide grid across the 71-ha island. After establishing protocols to avoid nontarget species, two island-wide applications of diphacinone rodenticide bait blocks took place in 2000. Post-treatment monitoring with bait stations indicated rats were eradicated by 2002 (Witmer et al. 2007). Week-long trapping sessions are conducted each December and Buck Island remains free of mongoose and rats. Vegetation restoration on Buck Island is also ongoing, and has consisted of manual removal of exotic plants, with guinea grass (*Megathyrsus maximus*) and Ginger Thomas (*Tecoma stans*) taking priority. Restoration also includes plantings of lignumvitae (*Guaiacum officinale*) and the native endangered agave, *Agave eggersiana*.

The history of a previous translocation of *A. polops* to Buck Island gave further confidence in its suitability as a translocation site. With imminent construction of a hotel on Protestant Cay, Philibosian and Ruibal introduced 16 individuals from Protestant Cay to Buck Island in 1968 (Philibosian & Ruibal 1971). Within 1 year, population increase was evident. Unfortunately, the population did not persist, presumably due to the continued presence of mongooses (Philibosian & Yntema 1976). For the present introduction, the northwestern beach-forest habitat of Buck Island was deemed the most appropriate translocation site; it was also the site of the translocation in 1968, and the site suggested by (Meier et al. 1990) and in NPS internal documents (Z. Hillis-Starr, unpublished data). The conditions on Buck Island, its protected status, institutionalized environmental monitoring, and the prior experience that *A. polops* could successfully be translocated made for convincing arguments that Buck Island was the optimal site for establishing a new population of *A. polops*.

Translocation Strategy

To implement the replicated soft-release protocol, we constructed eight adjacent 10 m × 10 m open-top enclosures on the northwest shore of Buck Island, approximately 20 m apart (Fig. 2). The enclosures were designed to confine the lizards in groups. Protection from predators was a minor concern in our case because there are no snake or mammal lizard predators on Buck Island, and we judged risks from avian predators such as American Kestrel (*Falco sparverius*) or Mangrove Cuckoo (*Coccyzus minor*) to be low. All enclosures were located underneath the beach-forest canopy. The substrate of all enclosures was dark sandy soil covered with dense leaf litter and woody debris. Leaf litter, herbaceous and shrubby vegetation, and dead woody debris provide refugia for *A. polops*. Enclosures were

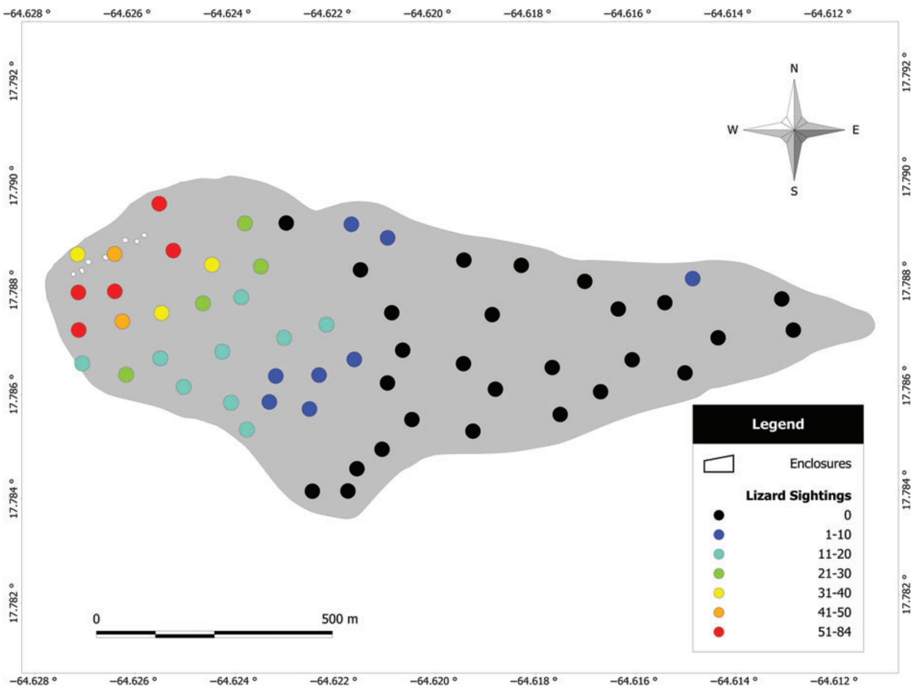

Figure 2. The population of *Ameiva polops* on Buck Island increased from 57 to about 1,400 individuals from 2008 to 2013. The map shows locations of the eight lizard enclosures, site occupancy, and lizard abundance in 2013. Colored symbols correspond to numbers of lizards counted during visual surveys that were used to create a population occupancy model. The numbers counted were largest near the enclosures, indicating a pattern of population spread eastward across the island.

25–50 m from the high water mark, on the inland side of the NPS trail. Four enclosures were constructed from Galvalume corrugated sheet metal (86 cm wide × 3.04 m and 2.43 m long) and four were made using DuraFlash® vinyl flashing which is cheaper, lighter, and easier to work with. The bottom 15 cm of the walls was buried to prevent *A. polops* from burrowing out. A PVC ledge was installed on the vinyl enclosures as an extra precaution, though there was no indication they could scale the walls. A gap was left in one wall of each enclosure until just prior to the translocation to minimize any enclosure effects.b A 2 m × 2 m grid laid out in the enclosures enabled us to note locations of lizards during behavioral monitoring.

Only individuals from Green Cay were used for the translocation for the dual reasons that this population is much larger than the critically small Protestant Cay population and to avoid mixing Protestant and Green Cay stocks. We captured a total of 65 *A. polops* on Green Cay by noosing (Fitzgerald 2012). Immediately after capture, lizards were held in wide-mouth insulated 2-L water coolers with a small ice pack and padding. Within approximately 1 hour of capture, lizards were brought to a processing area at the south end of Green Cay. At the processing area, they were placed in individual plastic containers within a 38-L cooler containing an ice pack. We took basic morphological data (Table 1) and determined sex by visual examination or by probing for hemipenes. Whether females were gravid was noted, as was general body condition. All translocated individuals were photographed, and scars and injuries were described in the notes. All individuals were marked by suturing colored glass

Table 1. Morphological traits of *Ameiva polops* introduced to Buck Island, St. Croix, U.S. Virgin Islands. Means and standard deviations are reported for the following measurements taken: SVL (length in millimeters from the tip of the snout to the cloaca); total tail length (TTL; length from the cloaca to the tip of the tail); regenerated tail length (RTL; length of total regenerated sections of tail, distinguished by a sharp change in pattern and color from the original tail); and mass (g).

	All	*Females (32)*	*Males (25)*
SVL	65.09 ± 5.71	63.09 ± 3.59	67.64 ± 6.87
TTL	117.9 ± 27.29	112.9 ± 23.09	124.3 ± 31.20
RTL	24.81 ± 27.73	26.84 ± 23.81	22.2 ± 26.12
Mass (g)	8.02 ± 2.30	6.98 ± 1.11	9.35 ± 2.73

beads to the dorsum of the tail and by toe-clipping. Toe-clips as well as a small segment of distal tail tissue (<10 mm) were preserved in 95% ethanol for subsequent population genetic analyses. Individuals deemed unnecessary for translocation were released at the site of capture on Green Cay. Capture periods ended at approximately 15:00 hours each day to allow time for processing and transport to Buck Island.

The *A. polops* were transported to Buck Island via a NPS vessel and placed into their assigned enclosures before 18:00 hours each day. We selected 57 (32 females and 25 males) sexually mature lizards (>50 mm snout-vent-length) in good body condition (i.e. no wounds, not thin, or emaciated) for translocation to Buck Island. We translocated more females than males because lizards in the genus *Ameiva* are polygynous and males can mate more than one female (Pianka & Vitt 2003).

We placed four females and three males into each of the eight enclosures. We presumed that during courtship, male *A. polops* guard receptive females (Fitzgerald 1994; Pianka & Vitt 2003), and assigned the one mated pair we captured to the same enclosure. An additional male was added to one enclosure after we observed a possible predation attempt by an American Kestrel or Mangrove Cuckoo, though the attacked individual was seen in good condition in subsequent surveys; thus, one enclosure had eight individuals (four males and four females). The density of *A. polops* in the enclosures was 700/ha (except for enclosure 1 with 800/ha), similar to densities reported for other island-dwelling teiids (Schall 1974; Treglia 2010).

Monitoring

Enclosure Monitoring. Behavior of the translocated lizards was monitored to assess how well they acclimatized to their new surroundings. One observer (MLT) conducted surveys of the enclosures by walking slowly around the perimeter of each enclosure for 10 minutes, identifying all *A. polops* that could be detected based on the bead combination and any other visible markings with the aid of 8-power binoculars and noting their behaviors. All surveys were conducted between 10:30 and 14:30 hours; the direction walked and the starting enclosure were alternated for each subsequent survey. The resulting dataset from these visual encounter surveys enabled us to evaluate the population-level activity. We also conducted focal observations on individuals, noting time of day, location, substrate, and behaviors based on descriptors employed by Lewis and Saliva (1987). Observations of individuals lasted up to 38 minutes, but most ended sooner when the subject was lost from sight (e.g. entered a burrow) or fled from the observer.

In the last week of monitoring, 3–10 July, 2008, we set pitfall traps to confirm the presence of individuals that had not been seen during daily surveys. Five pitfall traps made from 7.6-L plastic flower pots with 28 cm × 28 cm corrugated cardboard cover boards were installed in each enclosure, with one placed in the center, and the others 2.5 m interior of each corner. Traps were opened daily from 09:00 to 16:30 hours, and trapping was supplemented with noosing. A body condition index was calculated using the ratio of mass/snout-vent length (SVL; Dickinson & Fa 2000) and compared to that of the same individuals from their initial capture on Green Cay using a paired Wilcoxon signed-rank test.

Post-Release Monitoring. Monitoring was implemented to confirm establishment of the new population, to estimate population size, and to understand patterns of dispersal of lizards across Buck Island. During May–June 2009, 1 year after the translocation, a sample of individuals was captured by noosing to measure body condition. The 5-year survey took place during March–May 2013, during which time visual surveys were conducted at 61 sites randomly selected in ArcGIS 9.3.

The pattern of presence and absences at sites and number of individuals observed was used to estimate the population size and extent of occupancy across Buck Island. We used an unreconciled double-observer method to document the presence or absence of *A. polops* at each of the 61 sites, with at least four visits to each site (Riddle et al. 2010). All surveys were conducted between 11:30 and 14:30 hours. At each site, habitat variables were collected to serve as covariates in occupancy and population models: average and maximum operative temperature, substrate temperature, ground cover, leaf litter depth, percent soil moisture, percent clay, percent sand, elevation, and vegetation association. Operative temperature models were made with copper foil formed to the size and shape of a lizard with SVL of 75 mm and tail length of 90 mm. An iButton™ temperature logger was placed inside the models, which were painted primer gray and calibrated to match the body temperatures experienced by lizards in the field (Dzialowski 2005). We placed four operative temperature models 8 m from the center point of the survey site on a compass heading selected with a random number generator. The operative temperatures were collected every 10 minutes over the three survey days. We clipped the data from 08:00 to 17:00 hours to coincide with the activity period of the lizard. We computed the mean from all the four temperature models to create one average temperature and to find the maximum temperature available within each site. These habitat and temperature data were rasterized and calibrated to data from SSURGO (Soil Survey Staff), National Park Service Vegetation Maps (Moser et al. 2010), USGS Digital Elevation Model (Gesch 2007), and surface temperature derived from Landsat 8 (USGS 2013). The rasterized data were used as covariates in the population occupancy models. Abundance within all sites was calculated using binomial N-mixture occupancy models with detection held constant at 20.1%, the average across all 61 sites (Nichols et al. 2000). The total population estimate across the island was interpolated from the sites across 30 m^2 grid cells using the equations from the site occupancy models (Sillett et al. 2012). All analyses were completed using Program R version 2.14.1 (R Development Core Team 2011), and the models were implemented in program R using package "unmarked" (Fiske & Chandler 2011).

Results

In total, 57 *Ameiva polops* (25 males; 32 females) were translocated to Buck Island between 30 April and 9 May 2008 and confined in enclosures for 71 days, after which time the enclosures were opened. The enclosure materials were entirely removed on 16 July, 2008. Throughout the study, only one lizard was known to escape. It was seen outside of its enclosure and was thus excluded from analyses. Daily surveys throughout the release area yielded no evidence of any other escapes.

Enclosure Monitoring

We completed 26 timed visual surveys of all enclosures, during which we made 137 individual sightings of *A. polops* and positively identified 20 individuals. There were 32 sightings of individuals that could not be identified because the colored beads were not visible or were lost. The average number sighted on a survey was 5.28 (SD = 2.24; range = 2–10). No *A. polops* were ever seen in enclosures 4 and 7 (Table 2).

Table 2. Numbers of *Ameiva polops* identified and recaptured in enclosures during 26 visual surveys on Buck Island during 62 days of observation.

	Enclosure								
	Overall	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Known individuals (♀:♂)	32:25	4:4	4:3	4:3	4:3	4:3	4:3	4:3	4:3
Proportion of total seen	20/57 (35%)	4/8	1/7	3/7	0/7	2/7	5/7	0/7	5/7
Proportion of females seen	9/32 (28%)	1/4	1/4	2/4	0/4	0/4	3/4	0/4	2/4
Proportion of males seen	11/25 (44%)	3/4	0/3	1/3	0/3	2/3	2/3	0/3	3/3
Recaptures (♀:♂)	7:4	2:1	1:0	1:2	0:0	0:0	3:1	0:0	0:0

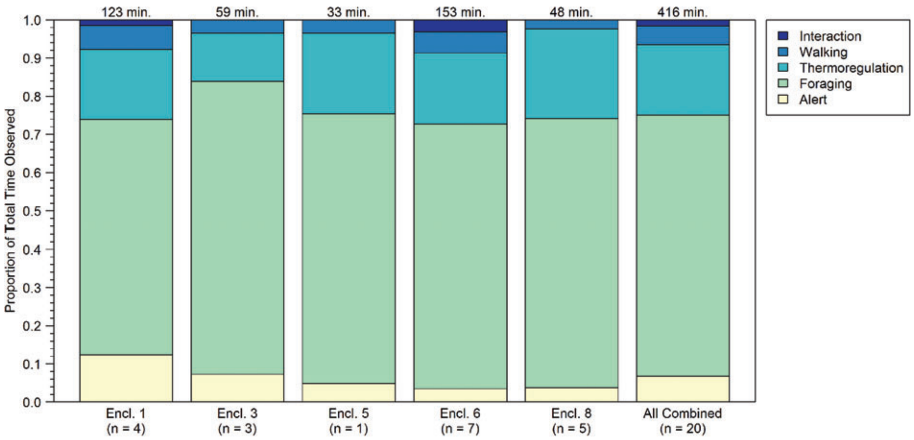

Figure 3. The behavior patterns exhibited by translocated lizards was similar among the five enclosures where lizards were observed. The proportion of each behavioral category is based on the total number of minutes lizards were observed in each enclosure.

During the enclosure period, we observed *A. polops* engaged in foraging, thermoregulating, and mate-seeking. No prior behavioral studies existed for *A. polops*, and our observations served the dual purposes of assessing the lizards' behaviors and also providing the first quantified behavioral observations on this species. We conducted 51 focal observations, primarily of 16 known individuals, including of both males and females, among five enclosures; other observations were of individuals that had lost beads and could not be positively identified. Individual observations ranged from 1.00 to 38.00 minutes (mean = 8.16; SD = 7.73). The total time observed per lizard ranged from 2.00 to 49.67 minutes (mean = 19.8; SD = 13.71) and all observations together spanned 415.97 minutes.

Foraging and thermoregulation were the dominant behaviors observed among all individuals in all enclosures (Fig. 3), accounting for an average of 64.36 and 22.42%, respectively, of the total activity time. Other behaviors included walking, being alert, and social interactions (<10% each). One mating event was documented during focal observations, in enclosure 6, and another was documented in enclosure 3. To compare behavior patterns among the enclosures, we visualized behaviors in a chart showing proportion of time spent in each behavioral category for each of the five enclosures where behaviors were observed, and for all observations combined. It was clear that there was no meaningful variation in lizard behaviors among enclosures. We did not perform statistical hypothesis tests on these data because of small sample size in each enclosure, and a statistical result would not enhance our biological interpretation of these data, that the lizards behaved similarly regardless of enclosure.

We recaptured 11 individuals at the end of the enclosure period to assess body condition. We did not disturb woody debris and leaf litter in the enclosures while searching for lizards. Turning over the habitat in the enclosures could have compromised the soft-release strategy, which was designed to allow individuals to become accustomed to the new location. There was no clear pattern of recaptures among the enclosures. We also did not recapture individuals in enclosures 5 and 8, but did observe two individuals in enclosure 5, and five individuals in enclosure 8 during the monitoring surveys (Table 2). We recaptured one individual in enclosure 2 that had never been seen during surveys. The sex ratio of recaptures was male-biased (seven males, four females), although sex ratios in the enclosures were female-biased (25 males, 32 females). At no time was body condition considered poor, but we did find that body condition of the recaptured lizards, as measured by the body condition index which takes into account size, improved significantly since initial translocation ($W = 51$, $p = 0.01367$). The mean increase in size-adjusted mass was 0.017 g (SD = 0.015). Ten of the 11 individuals recaptured increased in weight. The average weight at the time of translocation was 8.28 g (SD = 2.33), and was 9.61 g (SD = 2.74) at the end of the enclosure period.

In the final week of the enclosure period, we observed a hatchling in enclosure 2 that did not contain either of the two females noted as gravid upon translocation, indicating that an additional female was gravid when released, nested in the enclosure, and produced at least one offspring. Three days after the enclosures were removed, we saw another marked individual that was not seen during monitoring.

Post-Release Monitoring

Dispersal from the enclosure area was occurring by 2009. During visits to the translocation site for various reasons by NPS, USFWS, and USVI-DPNR biologists, and by us during May–June 2009, numerous *A. polops* adults (including gravid females), hatchlings, and juveniles were observed throughout the translocation site. During May–June 2009, we captured several adult males and gravid adult females that were not toe-clipped, which meant they had hatched on Buck Island. We recaptured two translocated males, 88 and 83 mm SVL, which were larger than any other *A. polops* documented in the literature (Meier et al. 1990; Henderson & Powell 2009). A male that hatched on Buck Island had already grown to be a large adult, measuring 78 mm SVL. As all translocated individuals were permanently marked by toe-clipping, captures of unmarked individuals proved that within 1 year since translocation, these individuals had hatched, grown to maturity, and successfully mated. All hatchlings and juveniles observed in May–June 2009 could only have hatched on Buck Island.

During the occupancy and population surveys conducted 5 years post-translocation in 2013, 73.1% of the observed lizards were adults and 23.9% were classified as juveniles. Sex could not be reliably determined for all individuals. The most highly ranked occupancy model ($N = 2{,}050$ models) accounted for 28.1% total Akaike information criterion (AIC) weight (AIC: 943.3), with the next two models absorbing 25.1 and 10.1% of AIC weight, respectively (Table 3). All models included distance from enclosure and leaf litter depth as important covariates. The top three models included average operative temperature. The top model also included coarse woody debris and average substrate temperature. The second-ranked model was similar to the top model, but excluded substrate temperature as a covariate (Table 3).

Detection probabilities differ for presence and absence surveys and population counts because the probability of detecting a single individual among many at a site is much higher than the probability of detecting all active individuals at a site. Detection probability for the presence of *A. polops* was 80.5% (CI: 65.5–89.9%), and the population was estimated to occupy 58.9% (CI: 46.4–70.4%) of Buck Island. Detection probability was lower for population counts, ranging from 18.5 to 32.1% across sites. Distance from the enclosures was a significant variable in predicting lizard abundance ($p < 0.001$). Lizard abundance was also highest in woodland sites ($p < 0.001$), and less numerous in manchineel forests ($p = 0.01$) or areas with relatively wet soil ($p < 0.001$). Detection was relatively low (<20%) when the land surface temperature was less than 34°C but increased with surface temperature. Detection was relatively high at sites with a large rather than low proportion of sandy soil. All other covariates were insignificant in explaining variation in abundance or detection of animals. Our top model estimated a population size of 1,473 (CI: 940–1,802) lizards on Buck Island in May 2013. The bootstrap p-value (500 runs) for the abundance estimate was $p = 0.46$, suggesting the estimate is robust. When mapped, these results showed a clear gradient in lizard density, which was highest near the translocation site, indicating a pattern of dispersal eastward across the island (Fig. 2). We identified 16 determining factors related to translocation strategy, species life history, environmental features, and population monitoring that enhanced the probability of success for this translocation (Table 4).

Discussion

By all measures, the translocation of *Ameiva polops* to Buck Island was successful. It was evident lizards in the enclosures adapted to their surroundings within a day. During the enclosure period, the reproductive cycle of the lizards was not disrupted and the size-adjusted body condition among 11 recaptured individuals improved significantly. We observed mating, and can conclude based on observation of a hatchling in an enclosure that females oviposited in an enclosure, and there was hatching success in the new habitat even before the enclosures were opened. The life history of *A. polops* was undescribed and many aspects of its natural history have not been studied. Based on our observations of unmarked gravid females and large unmarked males at the translocation site after 13 months, we learned that *A. polops* grow faster and reach sexual maturity sooner than anticipated; at least a portion of the individuals breed in no more than 1 year.

A surprising result from initial monitoring was how few lizards were seen despite the containment of seven individuals in relatively small (100 m^2) enclosures. Of the 56 individuals in enclosures (excluding the one escapee), the most observed during a survey of all eight enclosures was 10. Meaningful mortality estimates were not possible due to low recapture rate and low detection probability (≤ 0.251) during visual surveys (Treglia & Fitzgerald 2011).

There were no apparent differences in behavior patterns among the five enclosures where observations were made. There were zero observations and zero recaptures from enclosures 4 and 7 and no individuals were recaptured. There were no recaptures in enclosures 5 and 8, but multiple individuals were observed in those enclosures during monitoring surveys. In the two enclosures with zero observations and zero recaptures, we are unable to conclude whether all the lizards had died or were less detectable than in the other enclosures. Although some mortality was expected, 100% mortality in two enclosures seems unlikely. *Ameiva polops* is secretive, moving under leaf litter and forest debris. The observation of a marked individual from enclosure 2 after the enclosure period that had never been seen during surveys indicates that it had either escaped or simply was not seen during 26 surveys. There was no pattern in number of individuals seen over time in the 26 surveys, either overall or by enclosure. This result indicated that there was no obvious trend in mortality or escape that would have caused fewer lizards to be seen by the end of the enclosure period. The habitat was consistent among enclosures, and there were no obvious causes that could explain the variation in recaptures that we observed.

Table 3. Results from the top 10 population occupancy models, ranked by Akaike information criterion weights (w[AIC]). Avg OTM, average operative temperature; Avg surface, average surface temperature; Cover perc, canopy cover percent; CWD, coarse woody debris; Dist, distance from enclosures; LLd, leaf litter depth; Max OTM, maximum operative temperature; Max surface, maximum surface temperature. Greek letters denote the following: binomial detection (σ), negative binomial abundance distribution (λ), and dispersion parameter (α).

Population Occupancy Model Set	*Number of Parameters*	*AICc*	w*(AIC)*
λ (Avg surface + Avg OTM + Dist + LLd + CWD)$\sigma(.)\alpha$	7	943.3	0.281
λ (Avg OTM + Dist + LLd + CWD)$\sigma(.)\alpha$	6	943.5	0.251
λ (Avg surface + Avg OTM + Dist + LLd + Max OTM + CWD)$\sigma(.)\alpha$	8	945.3	0.103
λ (Dist + LLd + CWD)$\sigma(.)\alpha$	5	945.7	0.083
λ (Avg surface + Avg OTM + % Cov + Dist + LLd + CWD)$\sigma(.)\alpha$	8	946.1	0.067
λ (Avg surface + Avg OTM + Dist + LLd + Max surface + CWD)$\sigma(.)\alpha$	8	946.6	0.053
λ (Avg OTM + Cover Perc + Dist + LLd + CWD)$\sigma(.)\alpha$	7	946.7	0.05
λ (Avg OTM + Dist + LLd + Max surface + CWD)$\sigma(.)\alpha$	7	947	0.043
λ (Avg OTM + Dist + LLd + Max OTM + CWD)$\sigma(.)\alpha$	7	947.4	0.036
λ (Avg OTM + Dist + LLd + Max surface + CWD)$\sigma(.)\alpha$	6	947.5	0.033

Table 4. Factors identified as key determinants of successful translocation of *Ameiva polops* to Buck Island, U.S. Virgin Islands with references to supporting literature.

Factors Important in Translocation of Ameiva polops *to Buck Island*	*Supporting Literature*
Translocation strategy	
Clarity of goals	Seddon et al. (2007)
Selection criteria for translocation site	Wolf et al. (1998)
Interagency cooperation and funding	IUCN (1998)
Large propagule number	Griffith et al. (1989) and Wolf et al. (1998)
Female-biased sex ratio	Dodd and Seigel (1991) and (Burke 1991)
Selection of individuals (sexually mature adults)	Germano and Bishop (2009)
Soft-release enclosures	Bright and Morris (1994) and Teixeira et al. (2007)
Species life history traits	
Small body size	Dodd (1980)
Rapid growth to maturity	
Polygynous mating system	
Habitat and dietary generalist	
Environmental and biotic factors	
Habitat quality and quantity	Wolf et al. (1998)
Few predators	Dodd and Seigel (1991) and Wolf et al. (1998)
Few competitors	Wolf et al. (1998)
Monitoring factors	
Intensive monitoring during enclosure period	Treglia (2010) and Treglia and Fitzgerald (2011)
Systematic population assessment after population was established	

We are confident in concluding that this translocation of *A. polops* was successful in establishing a population on Buck Island. After 1 year, no marked individuals were seen but there were many unmarked adults and juveniles, and gravid unmarked females. We counted 354 individuals observed during the survey 5 years after post-translocation, hence at least two generations had been produced between 2008 and 2013 (assuming a generation time of 18–24 months). Population estimates indicated that the population grew from 57 to about 1,400 in 5 years.

We consider several factors as key determinants to this outcome. The life history of *A. polops* is a principal reason translocations seem to work for this species. *Ameiva polops* is relatively small, reaches sexual maturity, and breeds within a year, and is an ecological generalist. The second principal driver was eradication of mongoose and tree rats from Buck Island, a spectacular achievement by leaders in NPS that should be repeated throughout islands and locations in the Caribbean and elsewhere. *Ameiva polops* has persisted on Green, Protestant, and Ruth Cays because mongoose never occurred there. However, there are roof rats and house mice (*Mus musculus*) on these cays, and the extent to which they impact *A. polops* has not been assessed. However, more *A. polops* are found with damaged tails on Protestant Cay than in the new population on Buck Island, and it is possible the relatively high rate of tail injuries was partly due to rats and mice (Angeli 2012). The absence of roof rats on Buck Island likely also favors population growth and dispersal in *A. polops*.

Our approach to the translocation probably enhanced the likelihood of population establishment, rate of population growth, and dispersal. Our effort allowed for as large a propagule size as we could justify considering the rarity of *A. polops*. We considered the 32 females and 25 males a large number because population estimates on Green Cay have ranged from 183 to approximately 4,000 depending on survey methodology

(Treglia 2010). The Ruth Cay population was founded with 10 individuals, and 16 were used in the translocation to Buck Island in 1968 that showed promise but apparently failed due to mongoose predation (Philibosian & Yntema 1976). The replicated soft-release enclosures allowed us to contain movements of groups in manageable sized enclosures while also distributing them over a large portion of the high-quality beach forest in northwestern Buck Island. Smaller enclosures also facilitated monitoring of these small secretive lizards. Another recent translocation of a gecko species demonstrated that soft-release (penning) decreased immediate post-translocation movements, which could increase reproductive success and population growth (Knox & Monks 2014). Replicated enclosures have also been used in a translocation of Florida sand skinks (*Neoseps reynoldsi*) to facilitate monitoring and experimentation (McCoy et al. 2014). Dodd and Seigel (1991) recommended releasing individuals in groups that were similar to the population structure of the source population. Their recommendation may make sense in cases of long-lived organisms (but see Burke 1991), but in the case of relatively small, short-lived, fast-growing, ecological generalists such as *A. polops*, we suggest that our approach of using groups of adults in a female-biased sex ratio is more likely to speed population growth. In a review published after this translocation had taken place, Germano and Bishop (2009) identified homing and movements, insufficient numbers, and human collection as principal causes of failure in reptile translocations. Our design fortunately had accounted for these potential pitfalls a priori. Finally, the translocation may not have taken place at all without cooperation among USFWS, NPS, USVI-DPNR, and professional herpetologists.

Our results and experiences from the two previous historical introductions (Philibosian & Ruibal 1971; Knowles 1990) give every indication that *A. polops* is an excellent candidate for translocations. The translocation to Ruth Cay was successful despite a low propagule number, informal monitoring, a less concerted effort at rodent control, and smaller overall area of perceived high-quality habitat. Mongoose predation was undoubtedly the principal driver of extirpation of *A. polops*, and the failed introduction to Buck Island in 1968 highlights the high susceptibility of *A. polops* to this invasive species. The initial introduction to Buck Island (Philibosian & Ruibal 1971) showed clear signs of success. However, mongooses were not completely eradicated by the time of that translocation (Z. Hillis-Starr, unpublished data) and it is likely mongoose were the undoing of that translocation attempt (Philibosian & Yntema 1976). Interestingly, other small teiid species persist in the face of mongoose predation on a number of islands in the Caribbean, including *Ameiva wetmorei* in Puerto Rico, the sister taxon to *A. polops* (Hurtado et al. 2014). We hypothesize that behavior patterns specific to *A. polops*, perhaps selection of nocturnal refugia or escape behaviors, make them more susceptible than their congeners. These observations call for future research on susceptibility to mongoose predation in Caribbean *Ameiva* as well as research on foraging by mongoose. We also note that extensive sugar cane agriculture and other forms of habitat conversion were taking place throughout St. Croix concurrently with the decline of *A. polops*. Interactions between predation and habitat loss may have exacerbated the decline of *A. polops*, but cannot be understood in retrospect. Nonetheless, research designed to gain insight into interactions between habitat use by mongoose, habitat use by *A. polops*, and how the configuration of habitats affects their susceptibility to exotic predators would provide novel and important information useful to restoring populations of *A. polops* and other island endemics.

Funding and staffing were recently cited as major challenges hindering progress in translocations (Ewen et al. 2014). These challenges are pervasive and translocation literature has called for reporting monetary investment in translocations to make obstacles better understood (Griffith et al. 1989; Fischer & Lindenmayer 2000). However, dollar sums do not reflect the costs of integrated efforts to complete translocation projects such as the one reported here, that were carried out with meager financial resources. Moreover, long-term efforts directed to ecosystem restoration that are required prior to translocations can be extremely complex (e.g. the 30+ year mongoose eradication on Buck Island, rat eradication, and island-wide nonnative invasive plant program), making it virtually impossible to report costs in a way that is relevant to other cases. Monetary valuation of translocations could send confusing signals to conservation practitioners, and even discourage some efforts if translocation efforts are perceived to be expensive. Furthermore, monetary valuation creates the perception a market is created for conservation translocations, as exists for wildlife management translocations. The bottom line for costs of this translocation, and probably most other conservation translocations, was about making things work with existing resources and allocation of personal and professional priorities.

We are optimistic about the future of *A. polops* and its inclusion in restoration efforts on St. Croix. At this time, replicates of both Protestant Cay and Green Cay populations have been established on Ruth Cay and Buck Island. The new population on Buck Island is already larger than the other three populations combined, and the monitoring results show the population is continuing to expand across Buck Island. We suggest efforts to restore *A. polops* to appropriate sites on St. Croix be seriously considered for the near future. Carefully planned reintroductions of *A. polops* to St. Croix merit serious consideration. A strategy to reintroduce *A. polops* to St. Croix should take into account the distribution of mongoose on St. Croix to select sites where interactions between mongoose and *A. polops* can be minimized. Landscape-scale analyses can identify a number of sites on St. Croix where density of mongoose is relatively low, and where natural and artificial landscape features such as peninsulas and fencing around structures can be taken advantage of to exclude mongoose from small areas. *Ameiva polops* is a habitat generalist that can live in many areas of St. Croix where mongoose can be locally excluded and controlled. In the last decade, *Ameiva exsul* a large teiid from the Puerto Rican bank has become established on mainland of St. Croix. *Ameiva polops* is naïve to *A. exsul* and may be susceptible to predation from this exotic, which is known to consume other lizards (Treglia et al. 2013). *Ameiva exsul* should be eradicated from St. Croix to reduce chances for competitive interactions with *A. polops* and other native fauna. A program to reintroduce *A. polops* to St. Croix can take advantage of the interagency collaborations, natural history knowledge, and prior experiences that set the stage for the successful introduction to Buck Island. Reintroduction experiments can be undertaken at relatively low cost, carry almost no risk to the species, and help restore some of the native biodiversity to St. Croix.

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